

The songs of the western European bush-crickets of the genus *Platycleis* in relation to their taxonomy (Orthoptera: Tettigoniidae)

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SYNOPSIS. The calling songs of 11 species of the decticine genus *Platycleis* s.l. (including *Sepiana*, *Tessellana* and *Montana*) are described and fully illustrated with oscillograms at three or four different speeds. For each species a list is provided of references to any past work published on the songs, classified according to the kind of information given. Notes on recognition, using both morphology and song, are given for each species, and two identification keys are provided, one based on morphology and the other on song. The value of the song as a taxonomic character is discussed.

INTRODUCTION

The decticine bush-crickets, of which *Platycleis* is one of the most familiar Old World genera, are a group of usually cryptically coloured insects living on or near the ground, or occasionally in shrubs. The group includes over 160 European species, several of which are pests in parts of their range.

Platycleis, in the broad sense used here, is a widespread Palearctic genus including about 100 species, usually grey-brown or yellow-brown in

colour and living in open, mainly dry habitats at a wide range of altitudes. Eighteen species have been recorded from western Europe, of which at least two, *albopunctata* and *intermedia*, become pests when they occur in sufficient numbers, causing damage to cereal grasses and other crops.

As in most Tettigoniidae, the males of all species of *Platycleis* stridulate by rubbing a scraper on the right fore wing against a file on the underside of the left fore wing; the females are silent. The main function of the songs is to attract conspecific females and the differences between the songs provide a mate recognition system, as in

Table 1 Data for the field recordings of songs of *Platycleis* used for oscillograms reproduced in this study. Recordists' names are abbreviated as follows: DRR = D. R. Ragge; WJR = W. J. Reynolds; MJS = M. J. Samways. Further details are given on pp. 2–3.

Species	Locality	Date recorded	Recordist	Shade air temperature	Recording No.
<i>albopunctata</i>	FRANCE: Vaucluse, Mont Ventoux, road from Bédoin, 1100 m	12.viii.1977	DRR	20°C	234/4
	ITALY: Abruzzi, Gran Sasso d'Italia, 2 km E. of Passo delle Capannelle, 1500 m	2.ix.1985	DRR	21°C	605/1
<i>sabulosa</i>	FRANCE: Pyrénées-Orientales, St Cyprien	31.viii.1974	DRR	24°C	137/2
<i>affinis</i>	FRANCE: Vaucluse, near Carpentras, Bédoin	13.viii.1977	DRR	22°C	235/1
<i>romana</i>	ITALY: Lazio, near Rome, SE. side of Colli Albani	8.ix.1985	DRR	26°C	60e/9
	ITALY: Calabria, Sila Mountains, near Bocca di Piazza	20.ix.1988	DRR	16°C	725/3
<i>falx</i>	FRANCE: Hérault, Agde, Pic St Loup	3.viii.1972	MJS	19°C	243/8
	FRANCE: Pyrénées-Orientales, St Cyprien	31.viii.1974	DRR	24°C	137/1
	FRANCE: Hérault, near Montpellier, bank of Canal du Rhône	27.viii.1986	WJR	25°C	640/1

the true crickets and gomphocerine grasshoppers. The songs of the western European *Platycleis* provide an excellent means of recognizing the species in the field; this is especially useful as several of the species are extremely difficult to identify from their morphology. Although the songs of several species have been used as the basis of a number of behavioural studies (e.g. Samways, 1976a, 1976b, 1976d, 1977; Samways & Broughton, 1976; Latimer, 1981a, 1981b), and are included in the excellent work by Heller (1988) on the bioacoustics of European Tettigoniidae in general, there has been no comprehensive account of the songs of the species of *Platycleis* in relation to their taxonomy and identification. The main aim of the present paper is to provide such an account for the western European species. The paper is primarily concerned with Europe west of, and including, Germany, Austria and Italy, but most of the species treated also occur commonly in eastern Europe and some of them extend their ranges into Asia.

The only western European species not included in this study are very local forms, often of doubtful status, in which the song is unknown to me. For each of the 11 species included a list is

provided of references to any previously published information on the song, classified according to the kind of information published.

ABBREVIATIONS OF DEPOSITORIES

BMNH	British Museum (Natural History), London
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin
NM	Naturhistorisches Museum, Vienna

METHODS

RECORDING AND ANALYSING THE SONGS

With one exception, all the field recordings of the songs used in this study were made with a Uher 4000, 4200, 4200 IC or 4200 Monitor tape recorder

Table 2 Data for the indoor recordings of songs of *Platycleis* used for oscillograms reproduced in this study. Recordists' names are abbreviated as in Table 1. Further details are given on pp. 3–4.

Species	Locality	Date collected	Date recorded	Recordist	Air temperature	Recording No.
<i>albopunctata</i>	ENGLAND: Sussex, Eastbourne, Cow Gap	11.vii.1976	13.vii.1976	DRR & WJR	27°C	166
	WALES: West Glamorgan, Gower, Nicholaston					
	Burrows	3.ix.1976	6.ix.1976	DRR	24°C	173
	JERSEY: Quennevais	16.vii.1977	23.viii.1977	WJR	30°C	214
	SPAIN: Madrid, Sierra de Guadarrama, Puerto de Morcuera, 1796 m	15.ix.1982	28.ix.1982	WJR	26°C	467
<i>sabulosa</i>	SPAIN: Madrid, Manzanares	13.ix.1982	1.x.1982	WJR	22°C	472
	SPAIN: Toledo, near Oropesa, Las Ventas de San Julian	4.viii.1983	5.viii.1983	DRR	23°C	507/7
<i>affinis</i>	FRANCE: Landes, 3 km NW. of Morcenx	15.ix.1976	15.ix.1976	WJR	18°C	180/10
	SPAIN: Zamora, Benavente	21.viii.1986	21.viii.1986	WJR	27°C	586/4
<i>intermedia</i>	SPAIN: Granada, La Rábita	24.vi.1984	30.vii.1984	DRR	23°C	536
<i>sepium</i>	YUGOSLAVIA: Croatia, 2 km SE. of Rijeka	16.viii.1985	4.ix.1985	WJR	25°C	582
<i>tessellata</i>	FRANCE: Vaucluse, Mont Ventoux, near Les Bruns	11.viii.1977	11.viii.1977	DRR	24°C	233/5
	SPAIN: Madrid, Manzanares	13.ix.1982	30.ix.1982	WJR	22°C	473
<i>veyseli</i>	AUSTRIA: Burgenland, Neusiedler See, near Illmitz	18.viii.1973	19.viii.1973	DRR	26°C	102/2
<i>montana</i>	Same locality	24.viii.1973	24.viii.1973	DRR	25°C	104/1
	Same locality	24.viii.1973	26.viii.1973	DRR	25°C	104/2
<i>stricta</i>	ITALY: Abruzzi, Gran Sasso d'Italia, Valley N. of Monte della Scindarella, 1800 m	1.ix.1985	1.ix.1985	DRR	25°C	604/5

and AKG D202 microphone; the exception, recording 243/8, was made with an Akai X-IV tape recorder and Akai ADM-4 microphone. The tape speed was always 19 cm/s. All the recordings were made while the insects were in full sunshine except for recordings 640/1 and 725/3, which were made during hazy sunshine, and recording 243/8, which was made at night in complete darkness. Recording 243/8 was made from a caged insect (collected 8 days previously) in the open air; all the other recordings were made from free insects (captured

immediately after the recording) that were approached stealthily so that the microphone could be held (or rested on the ground) close to them without causing any disturbance.

The indoor recordings were made in a suitable quiet room near the original locality using a Uher tape recorder and AKG microphone of the type mentioned above (tape speed: 19 cm/s), or in the BMNH Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH 405 microphone (tape speed: 19, 38 or 76 cm/s).

Recordings 507/7 and 586/4 were made in complete darkness, recordings 102/2, 233/5, 536 and 582 were made in dim light, and the remaining recordings were made with a bench lamp next to the cage to provide light and radiant heat.

Further details are given in Tables 1 and 2 for the recordings used for the oscillograms reproduced in Figs 36–125. However, the song descriptions given for each species are in most cases based on many more recordings of numerous songs, all of which were analysed oscillographically. The oscillograms reproduced in the figures were chosen as being typical of the species concerned and, in some cases, showing the extent of intra-specific variation.

All the oscillograms were made from recorded songs with a Mingograf 34T ink-jet recorder.

SONG TERMINOLOGY

The bio-acoustic terms used are defined as follows. *Calling song*. The song produced by an isolated male.

Syllable. The sound produced by one complete opening and closing movement of the fore wings (Fig. 1). The songs of a number of European decicline bush-crickets include two contrasting kinds of syllable, differing markedly in duration. Following Samways (1976a) I have termed the longer, more normal ones *macro-syllables* and the shorter ones, usually lasting less than 10 ms, *microsyllables* (Fig. 1).

Diplosyllable. A syllable in which sound is produced by both the opening and closing movements of the fore wings (Fig. 1).

Hemisyllable. The sound produced by one uni-directional movement (opening or closing) of the fore wings (Fig. 1 and see below).

Echeme. A first-order assemblage of syllables (Fig. 1 and see below).

Echeme-sequence. A first-order assemblage of echemes.

For convenience in describing the songs of *Platycleis* the definition of the term hemisyllable given above is slightly looser than that given by Broughton (1964: 853). Broughton took the view that this term should be used only in referring to each of the two components of a diplosyllable, i.e. when sound is produced by both the opening and closing movements of the fore wings; he suggested the term 'haplosyllable' for a syllable in which sound is produced by only one of the two movements of the fore wings (usually the closing stroke). In several species of *Platycleis* the open-

ing strokes of the fore wings sometimes produce sound but sometimes do not; using Broughton's definition the sounds produced by the closing strokes would sometimes be hemisyllables and sometimes haplosyllables, and description would become too cumbersome. The definition of hemisyllable given above removes this difficulty. In songs containing both micro- and macrosyllables I have further simplified the terminology by sometimes referring to 'closing macrosyllables' when 'closing macrohemisyllables' would be strictly more accurate.

The simple definition of the term echeme given above gives rise to some difficulty in two species of *Platycleis*: *stricta* and *montana*. The song of *stricta* includes a dense series of equally spaced syllables in which every third one is louder than the rest (Figs 122, 124). It could be argued that these units of one louder and two softer syllables (or even just the two softer ones) are first-order assemblages of syllables and that they should therefore be termed echemes, but I have found it less cumbersome in the present study to regard the complete series of syllables as a single echeme. In effect, this interpretation requires the presence of distinct pauses as a criterion for separating groups of syllables into echemes, rather than the mere repetition of a pattern based solely on changes in amplitude. I have used the same criterion in treating the dense series of syllables produced by *montana* as echemes, although the syllables are alternately softer and louder (Figs 117–120).

PRESENTATION

As the main purpose of this paper is to give information on songs, I have not included either a full synonymy or a formal morphological diagnosis in the account of each species. I have, however, listed references to all past descriptive accounts of the songs (of any significance), classified according to whether they include oscillograms (including sound-level tracings), diagrams (i.e. hand-drawn representations of the songs), sonagrams (audiospectrograms), frequency information, musical notation, or verbal description without any of these additions; any commercially available disc or cassette recordings of the songs are also listed. These references are not intended to be exhaustive – there are many brief statements about the songs, especially in the earlier literature, that do not warrant inclusion; my aim has been to list all sources that the reader might find useful to refer to for additional or confirmatory information on the songs. The only references I have included to works published before the

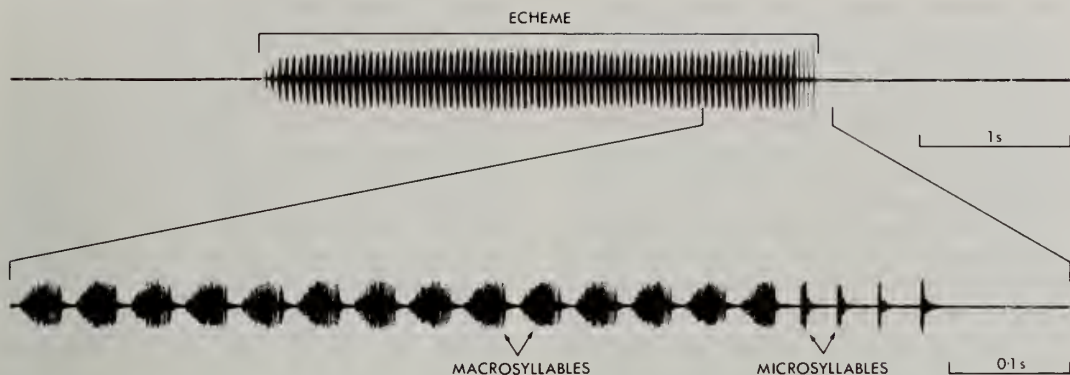
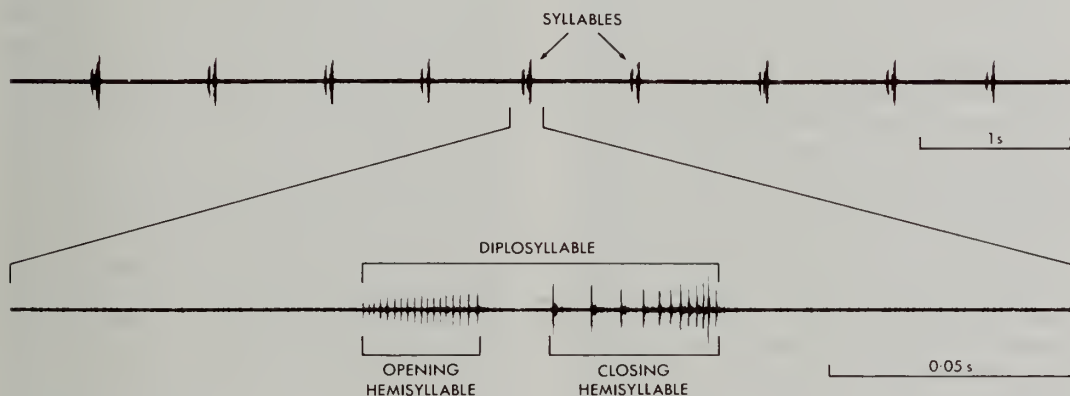
*Platycleis falx**Platycleis veysseli*

Fig. 1 Oscillograms of the male calling songs of two species of *Platycleis*, showing the terminology used in this paper.

present century are to two papers by Yersin (1854b, 1857), the first of which gives a short but admirable account of the songs of 38 European species of Orthoptera (including two of *Platycleis*), in which he attempted, with some success, to represent them in terms of musical notation.

Notes are given for each species on recognition by both morphology and song, and these are followed by a more detailed descriptive account of the calling song. The songs of Tettigoniidae, unlike those of most gomphocerine grasshoppers, are often produced after dark as well as during the day, and as a result these insects sing over a very wide range of body temperatures. During low night-time temperatures the muscles of the stridulatory organ move much more slowly than in sunny daytime weather and, although the overall rhythmic pattern of the song is usually maintained, the repetition rates for syllables and

echemes become much lower (cf. Figs 90, 92). In addition, the songs of the small species of *Platycleis* included in this study (*tessellata*, *veysseli*, *montana* and *stricta*) are too quiet to be heard by the human ear in most outdoor situations. The song descriptions given in this paper for each of the larger species refer to songs produced in warm, sunny, daytime weather; those given for the four small species refer to songs produced by captive males in quiet, warm, indoor conditions, especially at night.

Tettigoniid songs usually contain a large element of ultrasound; in many species most of the sound energy is ultrasonic and a few tettigoniid songs are entirely ultrasonic. Even the audible frequencies tend to be towards the higher end of the audio range and some human ears with poor high-frequency reception are quite unable to detect them. All the species of *Platycleis* included in this

study produce songs that are clearly audible to anyone with good high-frequency hearing, and the audible sound contains all the information (mainly the rhythmic pattern) needed for taxonomic use. All the descriptions and oscillograms given in this paper are based entirely on the audible component of the songs (i.e. below 20 kHz in frequency).

The songs of each species are illustrated by oscillograms at three (in one instance four) different speeds. As the scale lines indicate, the three speeds normally given are (after reduction for printing) 20 mm/s, 160 mm/s and 640 mm/s. For two songs of *albopunctata* I have included oscillograms at the additional speed of 2560 mm/s in order to show the individual tooth-impacts of the stridulatory organ with particular clarity.

EXAMINATION OF THE TITILLATORS

The sclerotized epiphallallic structures generally referred to as 'titillators' are frequently useful in identifying male decicline bush-crickets. In dried specimens they are usually concealed (except sometimes for the apical parts) and the tip of the abdomen must be thoroughly relaxed before attempting to examine them; they can then be eased into an exposed position with the aid of fine forceps and either examined *in situ* or cut free from the surrounding tissues. Titillators removed from the abdomen may be preserved dry by being stuck to a small piece of card with a water-soluble adhesive, or immersed in glycerine in a small vial; the card or vial should then be attached to the same pin as the main body of the specimen.

CLASSIFICATION AND NOMENCLATURE

The taxonomy of the decicline bush-crickets belonging to *Platycleis* and related genera still defies a satisfactory solution after two centuries of study by many European workers. For the period 1852 to 1927 the genera *Platycleis* s.l. and *Metrioptera* Wesmael s.l. were united in a single genus, the name *Platycleis* being used until Caudell's work of 1908 and the earlier name *Metrioptera* being used, correctly, from that time onwards. Then Ramme (1927) proposed that *Platycleis* should be given separate generic status for its type species *grisea* and eight closely related fully winged species, leaving the name *Metrioptera* for the remaining very mixed assemblage of

species; he admitted that the generic assignment of such small fully winged species as *stricta*, *montana* and *tessellata* was uncertain.

This unsatisfactory situation lasted until 1941, when Zeuner produced what has been by far the most comprehensive taxonomic study of the group. Zeuner took the view that the problems presented by the classification of these insects could be solved only by distributing the species among a large number of small genera, and he proposed no fewer than 13 new genera in order to achieve this. These proposals proved to be too extreme for most European orthopterists, who have treated all but four of these new genera as subgenera of *Platycleis* or *Metrioptera*. I agree with the currently prevailing view that Zeuner's genera are better treated as subgenera, and am inclined to give *all* of them this status (together with *Eumetrioptera* Miram, 1935 and *Zeuneriana* Ramme, 1951), thus leaving *Platycleis* and *Metrioptera* as the only valid European genera in the group. This bipartite division is in itself unsatisfactory, since even these two genera cannot be clearly separated, but it is perhaps justified on grounds of convenience, at least for the time being, especially as *Metrioptera* is the earlier name. Taking this broad view I have included Zeuner's *Sepiana*, *Tessellana* and *Montana* in *Platycleis*, and hence in this present study. I agree with the view of both Zeuner (1941) and Ramme (1951) that *Sepiana* belongs to the 'Platycleis-group', and am therefore treating it as a subgenus of *Platycleis* rather than *Metrioptera*. (See also p. 8.)

Koçak (1984) has recently proposed replacement names for *Locusta tessellata* Charpentier and *L. vittata* Charpentier, both of which he believed to be junior primary homonyms. He was, however, wrong in thinking that *L. tessellata* Charpentier was preoccupied by '*Locusta tessellata* Drury', perhaps basing his belief on the erroneous statements by both Walker (1869: 171) and Kirby (1906: 144) that Drury's *tessellata* was originally described in *Locusta*. In fact Drury (1773: [92]) used the original combination *Gryllus* (*Acheta*) *tessellata* (not, as recently stated by Kruseman (1989: xi), '*Gryllus* (*Locusta*) *tessellata*'), and so there is no primary homonymy between these two names and the replacement name *emrahi* Koçak becomes a junior objective synonym of *tessellata* Charpentier (see p. 28). Koçak was, on the other hand, correct in thinking that *L. vittata* Charpentier was a junior primary homonym of *L. vittata* Thunberg, and so the currently valid name for *vittata* Charpentier is the replacement name *veyseli* Koçak (see p. 28).

The subgeneric assignment of the species included in the present study is shown below.

- Platycleis* (*Platycleis*) *albopunctata* (Goeze)
P. (P.) sabulosa Azam
P. (P.) affinis Fieber
P. (P.) romana Ramme
P. (P.) falx (Fabricius)
P. (P.) intermedia (Serville)
P. (Sepiana) sepium (Yersin)
P. (Tessellana) tessellata (Charpentier)
P. (T.) veyseli Koçak (= *P. vittata* (Charpentier))
P. (Montana) montana (Kollar)
P. (M.) stricta (Zeller)

Harz (1969) recognized about a dozen subspecies among the species of *Platycleis* s.l. included in this study. As Harz pointed out, many of these are based on inadequate material and most if not all of them are, in my view, better regarded as no more than local forms. I have been able to record and study the songs of several of these nominal subspecies and have found no differences from the songs of more typical populations. I have also decided (in agreement with Heller, 1988) to treat *grisea* as being no more than subspecifically distinct from *albopunctata* on the following grounds: (a) the two taxa are parapatric, (b) the morphological differences between them (solely in genitalia) are slight, (c) populations from the zone of contact seem to be morphologically intermediate, and (d) there is no apparent difference in the songs. Thus *grisea* reverts to the status it had before Zeuner (1940, 1941) first took the view that it was specifically distinct from *albopunctata*. Experimental studies on interbreeding between these two forms would be most useful.

THE SONG AS A TAXONOMIC CHARACTER

I have recently outlined the history of the use of the songs of Orthoptera in taxonomy (Ragge, 1986: 219–220). Much of the early work on the songs of Tettigoniidae was carried out in North America, where the pioneering studies of Scudder (1867, 1868, 1893) deserve a special mention. Like Yersin (1854b), who worked a little earlier in Europe, Scudder portrayed the songs he described in the form of musical notation. In 1932 Fulton produced keys to the Tettigoniidae and Gryllidae of North Carolina based on their songs, again a little later than the first attempt to do likewise in Europe (Faber, 1928). In each case it is

highly improbable that the Americans were aware of the work by their European counterparts.

The taxonomic value of the male calling songs of the western European species of *Platycleis* can be seen at a glance from Figs 36–48. There is a wide range of patterns from the regularly repeated short echemes of *albopunctata* and *sabulosa* to the mixture of short and quite different, long echemes of *stricta*. The seven larger species, from *albopunctata* to *sepium*, have songs consisting of a series of well-defined echemes; microsyllables are regularly produced by *affinis*, *romana* and *falx*, but are exceptional or completely lacking in the songs of the other four. In the songs of two of the smaller species, *tessellata* and *veyseli*, there are no well-defined echemes and no microsyllables: the syllables are either grouped into very loose and irregular echemes or are produced in long, even sequences of indefinite duration. The other two small species, *montana* and *stricta*, produce well-defined echemes; those of *montana* are of uniform duration and have no microsyllables, but those of *stricta* consist of a series of short echemes with microsyllables, interspersed with longer ones in which microsyllables may or may not be present.

Among the larger species, *falx* stands alone in producing echemes of at least 25 syllables and of fairly uniform duration within one song. The remaining six large species fall into three pairs: *intermedia* and *sepium* both produce disyllabic echemes, *albopunctata* and *sabulosa* produce echemes of 3–7 syllables (but an almost constant number within one song), and *affinis* and *romana* produce a mixture of short and long echemes in the same song. The similarities in the songs of *intermedia* and *sepium* are certainly no indication of affinity as these species differ markedly in morphology. However, the members of each of the other two pairs may well be fairly closely related to each other, especially *albopunctata* and *sabulosa*, which are largely allopatric and have probably diverged fairly recently.

I have been unable to find any significant difference between the songs of *tessellata* and *veyseli*. These two species are also very similar in morphology, differing mainly in wing-development, and are largely allopatric. They are almost certainly sister species that have evolved quite recently from a common ancestor, and it would be most interesting to find out experimentally whether they will readily hybridize.

The last two species, *montana* and *stricta*, are also largely allopatric and show some similarities in both song and morphology, but the relationship is much less close than in *tessellata* and *veyseli*.

The difficulties mentioned on p. 6 in defining *Platycleis* and *Metrioptera* as separate genera on

morphological grounds are reflected by the songs. The species of *Metrioptera* s.l. show a similar variety of song-patterns, some including micro-syllables and matching the songs of *Platycleis* species quite closely.

PLATYCLEIS Fieber

Chelidoptera Wesmael, 1838: 591 [as subgenus of *Decticus* Serville]. Type species: *Locusta grisea* Fabricius [now a subspecies of *P. albopunctata* (Goeze)], by subsequent designation (Kirby, 1906: 203). [Homonym of *Chelidoptera* Gould, 1836: 81.]

Platycleis Fieber, in Kelch, 1852: 5. Type species: *Locusta grisea* Fabricius [now a subspecies of *P. albopunctata* (Goeze)], by subsequent designation (Kirby, 1906: 203).

DIAGNOSIS. ♂♀. Pronotal disc fairly flat, with median carina in at least metazona. Fore tibiae with three external dorsal spurs. Brachypterous to macropterous. Male cerci with single internal tooth. Female subgenital plate with either median groove or median carina. Ovipositor upcurved. General colour usually grey-brown or yellow-brown.

DISCUSSION. The more typical fully winged, grey-brown members of the genus are easy to recognize as belonging to *Platycleis*. Partly green, brachypterous bush-crickets, in which the female subgenital plate lacks either a median groove or a median carina but which are otherwise very similar to *Platycleis*, are likely to belong to *Metrioptera*, but there is no clear dividing line between these two genera.

The male calling songs show a wide range of patterns in *Platycleis*, as discussed on p. 7, and are of little diagnostic value at the generic level. As in *Metrioptera*, microsyllables (see p. 4) are present in the songs of a number of species.

The subgenera are discussed on p. 6.

DISTRIBUTION. Europe as far north as southern Scandinavia, the whole of the Mediterranean Region, temperate Asia as far as China, including Kashmir and the extreme north of Pakistan; Azores, Madeira and Canary Islands.

INCLUDED SPECIES. As discussed on p. 6 I prefer to regard all the new genera proposed by Zeuner (1941) in his 'Platycleis-group', together with *Eumetrioptera* Miram, as subgenera of *Platycleis*. All these nominal genera have been previously treated as subgenera except, as far as I know, for the following, which I am here formally reducing in rank to subgenera of *Platycleis*: *Semenoviana*

Zeuner stat. n., *Squamiana* Zeuner stat. n., *Sporadiana* Zeuner stat. n. and *Eumetrioptera* Miram stat. n. *Alticolana* Zeuner was cited by Bei-Bienko (1951: 162) as a subgenus of *Metrioptera*, but as it belongs to Zeuner's *Platycleis*-group I am treating it here as a subgenus of *Platycleis*.

The currently valid species of *Platycleis* are listed below, segregated alphabetically under their respective subgenera. As indicated in the list, 19 specific names are newly combined with *Platycleis* as a result of the reduction in rank to subgenus of the genera with which they were formerly combined.

Genus *Platycleis* Fieber, 1852

Subgenus *Platycleis* Fieber, 1852

affinis Fieber, 1853
albopunctata (Goeze, 1778)
alexandra (Uvarov, 1927)
concii Galvagni, 1959
curvicauda Podgornaya, 1988
escalerai Bolívar, 1899
falx (Fabricius, 1775)
fatima Uvarov, 1912
iberica Zeuner, 1941
iljinskii Uvarov, 1917
intermedia (Serville, [1838])
irritans Ramme, 1951
kabulica Bei-Bienko, 1967
kashmira (Uvarov, 1930)
latitabunda Stolyarov, 1969
longicauda (Tarbinskii, 1930)
meridiana Stolyarov, 1969
pamirica (Ramme, 1930)
pathana Zeuner, 1941
ragusai Ramme, 1927
romana Ramme, 1927
sabulosa Azam, 1901
sinuata Ramme, 1951
sogdiana Mishchenko, 1952
trivittata Bei-Bienko, 1951
waltheri Harz, 1966

Subgenus *Squamiana* Zeuner, 1941

kurmana (Ramme, 1951) **comb. n.**
squamiptera Uvarov, 1912
weidneri (Demirsoy, 1974) **comb. n.**

Subgenus *Alticolana* Zeuner, 1941

alticola (Tarbinskii, 1930) **comb. n.**
atroflava (Bei-Bienko, 1951) **comb. n.**

Subgenus *Eumetrioptera* Miram, 1935

beybienkoi (Bekuzin, 1978) **comb. n.**
mistshenkoi (Bekuzin, 1961) **comb. n.**
monochroma (Bei-Bienko, 1947) **comb. n.**
obuchovae (Mishchenko, 1949) **comb. n.**
pavlovskiyi (Miram, 1935) **comb. n.**

Subgenus *Sepiana* Zeuner, 1941

sepium (Yersin, 1854))

- Subgenus *Tessellana* Zeuner, 1941
lagrecai (Messina, 1979) **comb. n.**
nigrosignata (Costa, 1863)
orina (Burr, 1899)
seniae Finot, 1893
sporadarum (Werner, 1933)
tessellata (Charpentier, 1825)
veyseli Koçak, 1984
- Subgenus *Incertana* Zeuner, 1941
chopardi (Jannone, 1936)
erecta (Uvarov, 1939)
incerta Brunner, 1882
persica Uvarov, 1917
- Subgenus *Parnassiana* Zeuner, 1941
chelmos (Zeuner, 1941)
coracis Ramme, 1920
dirphys (Willemse, 1980)
fusca Brunner, 1882
gionica (La Greca & Messina, 1976)
menalon (Willemse, 1975)
nigromarginata Willemse & Willemse, 1987
panaetolikon (Willemse, 1980)
parnassica (Ramme, 1926)
parnon (Willemse, 1980)
tymphiensis (Willemse, 1973)
tymphrestos (Zeuner, 1941)
vicheti (Delmas & Rambier, 1950)
- Subgenus *Decorana* Zeuner, 1941
arabica Popov, 1981
buxtoni (Uvarov, 1923) **comb. n.**
capitata Uvarov, 1917
concinna (Walker, 1869) **comb. n.**
decorata Fieber, 1853
himalayana (Ramme, 1933) **comb. n.**
kabila Finot, 1893
yalvacı (Demirsoy, 1974) **comb. n.**
- Subgenus *Sporadiana* Zeuner, 1941
brevipes (Uvarov, 1934) **comb. n.**
- Subgenus *Semenoviana* Zeuner, 1941
plotnikovi Uvarov, 1912
similis (Tarbinskii, 1930) **comb. n.**
tadzhika (Bei-Bienko, 1933) **comb. n.**
tamerlana (Saussure, 1874) **comb. n.**
tricarinata (Tarbinskii, 1930) **comb. n.**
- Subgenus *Montana* Zeuner, 1941
ankarensis (Karabağ, 1950)
armeniaca (Ramme, 1930)
barretii Burr, 1912
bifoveolata (Karabağ, 1950)
carpetana Bolívar, 1887
daghestanica Uvarov, 1917
decticiformis Shchelkanovtsev, 1914
dubia Uvarov, 1910
elegans (Uvarov, 1934)
eversmanni (Kittary, 1849)
heinrichi (Ramme, 1929)
macedonica (Berland & Chopard, 1922)

- medvedevi* (Miram, 1927)
montana (Kollar, 1833)
montenegrina (Ramme, 1933)
richteri Bei-Bienko, 1958
schereri Werner, 1901
striata (Kittary, 1849)
stricta (Zeller, 1849)
taurica Bolívar, 1899
tianshanica (Uvarov, 1933)
tomini Pylnov, 1916
uvarovi (Karabağ, 1950)
- Subgenus *Modestana* Beier, 1955
ebneri (Ramme, 1926)
kraussi Padewieth, 1900
modesta Fieber, 1853

KEYS TO THE PRINCIPAL WESTERN EUROPEAN SPECIES OF *PLATYCLEIS*

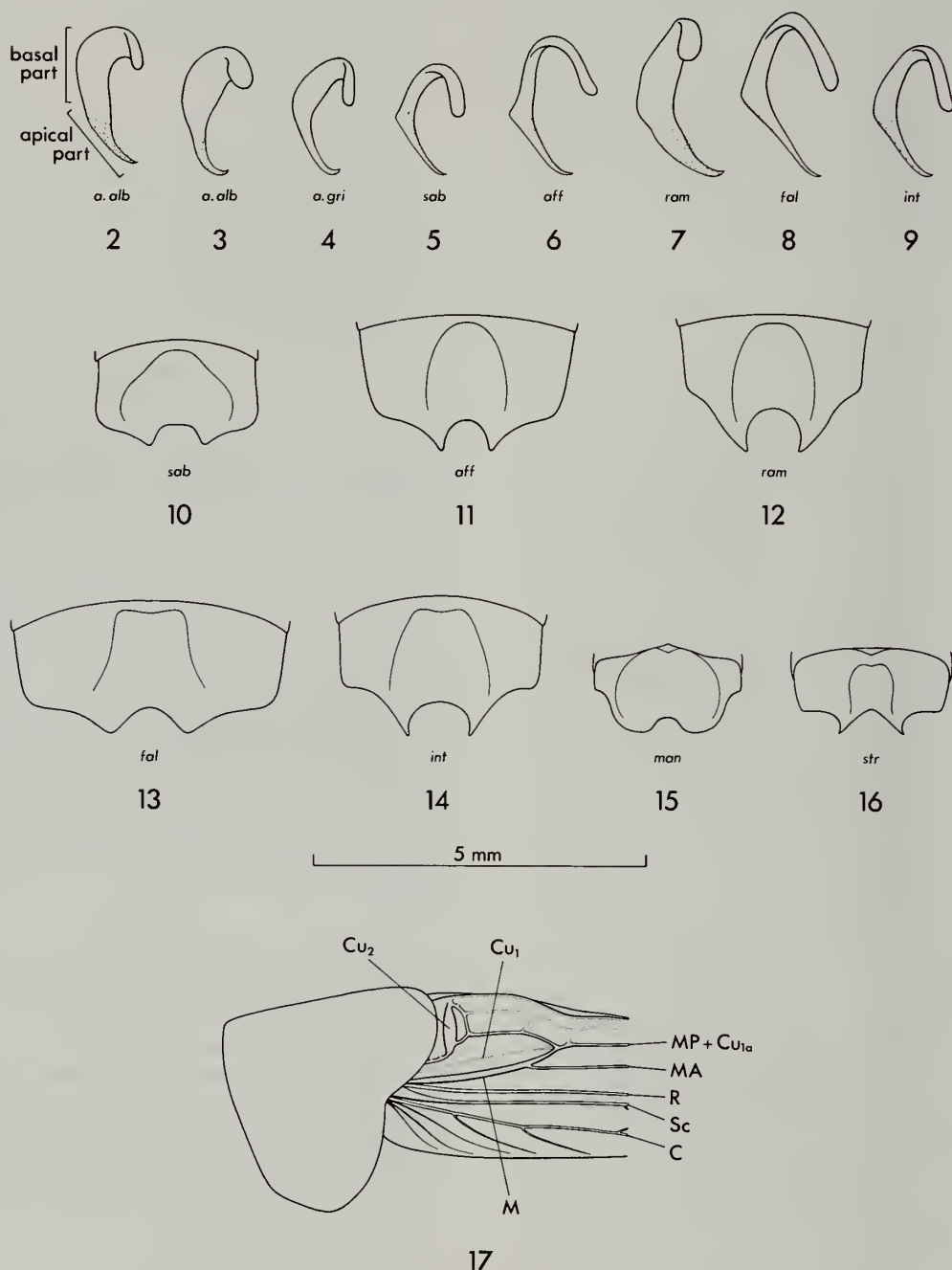
The only western European species not included in these keys are very local forms, often of doubtful status, in which the song is unknown to me.

Two keys are provided here, one based on morphological characters and the other on the male calling songs. Several of the larger species are very difficult to separate morphologically and, in the absence of song information, some specimens may not be correctly identified using the morphological key. Reference should in any case always be made to the notes on recognition given in the accounts of each species. *For reliable identification the song should be used whenever possible.*

KEY BASED ON MORPHOLOGICAL CHARACTERS

This key is for adults that are freshly collected or well preserved, particularly without undue shrinkage at the tip of the abdomen. The male tenth abdominal tergite is especially liable to collapse on drying, thus obscuring the useful specific characters that it otherwise shows; this is also true, to a lesser extent, of the female subgenital plate. For the method of examining the male titillators see p. 6. Males of the larger species, especially *sabulosa*, *affinis* and *intermedia*, are particularly difficult to identify from morphological characters, and associated females should be used for identification whenever possible.

- 1 Brachypterous, the fore wings not reaching the tip of the abdomen and the hind wings not reaching the tips of the fore wings2



Figs 2–17 Male genitalia and stridulatory organ of species of *Platycleis*. 2–9. Dorsal view of the right titillator of (2) *P. albopunctata albopunctata* (eastern Pyrenees), (3) *P. a. albopunctata* (southern Spain), (4) *P. a. grisea*, (5) *P. sabulosa*, (6) *P. affinis*, (7) *P. romana*, (8) *P. falx*, (9) *P. intermedia*. 10–16. Dorsal view of the male tenth abdominal tergite of (10) *P. sabulosa*, (11) *P. affinis*, (12) *P. romana*, (13) *P. falx*, (14) *P. intermedia*, (15) *P. montana*, (16) *P. stricta*. 17. Dorsolateral view of the stridulatory area of the left male fore wing of *P. affinis*, showing the wing-vein terminology used in this paper. Note that the male tenth abdominal tergite collapses in some dried specimens, after which its appearance can be quite different from that shown in Figs 10–16.

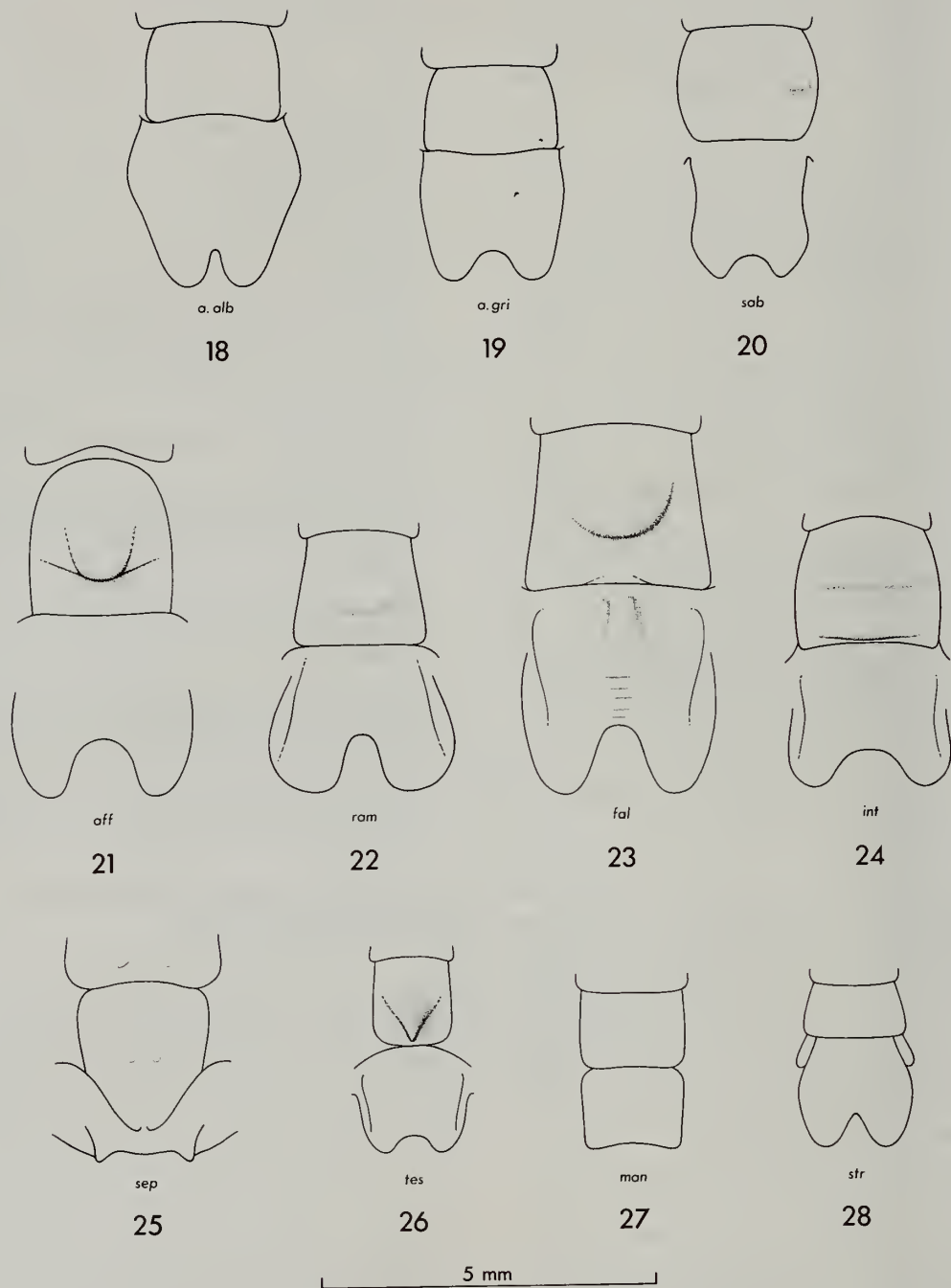
- Fully winged, the fore wings reaching beyond the tip of the abdomen and the hind wings reaching the tips of the fore wings3
- 2 Smaller: length of the pronotum less than 5 mm; length of the hind femora less than 18 mm .. *veyseli*
- Larger: length of the pronotum more than 6 mm; length of the hind femora more than 22 mm *sepium*
- 3 Male4
- Female13
- 4 Smaller: length of the pronotum less than 5 mm; length of the hind femora less than 17 mm5
- Larger: length of the pronotum more than 5 mm; length of the hind femora more than 17 mm7
- 5 Inner tooth of the cerci nearer the tip than the base..... *tessellata*
- Inner tooth of the cerci nearer the base than the tip6
- 6 Tenth abdominal tergite with rounded lobes (Fig. 15)..... *montana*
- Tenth abdominal tergite with pointed lobes (Fig. 16)..... *stricta*
- 7 Larger: length of the pronotum more than 6.5 mm; length of the hind femora more than 26 mm. Tenth abdominal tergite shaped as in Fig. 13 *falx*
- Smaller: length of the pronotum usually less than 6.5 mm; length of the hind femora less than 26 mm. Tenth abdominal tergite not shaped as in Fig. 13 ..8
- 8 Titillators with relatively broad basal part, as in Figs 2-4 or 79
- Titillators with relatively narrow basal part, as in Figs 5,6 or 911
- 9 From Italy10
- Not from Italy *albopunctata*
- 10 Titillators with relatively robust apical part, as in Fig. 7 *romana*
- Titillators with relatively slender apical part, as in Fig. 4 *albopunctata*
- 11 Lobes of the tenth abdominal tergite not sharply pointed, as in Fig. 10 *sabulosa*
- Lobes of the tenth abdominal tergite fairly sharply pointed, as in Figs 11 or 1412
- 12 *M* of the fore wings conspicuously pale-coloured at the base (see Fig. 17) *affinis*
- *M* of the fore wings not conspicuously pale-coloured at the base *intermedia*
- 13 Ovipositor less than 6 mm long, sharply curved upwards from near the base, as in Fig. 33 ... *tessellata*
- Ovipositor more than 7 mm long, not shaped as in Fig. 3314

- 14 Seventh abdominal sternite completely unmodified as in Figs 18, 19, 27 or 2815
- Seventh abdominal sternite with one or more swellings or ridges, as in Figs 20-2417
- 15 Subgenital plate truncate, as in Fig. 27 ... *montana*
- Subgenital plate clearly bilobed, as in Figs 18-24 or 28.....16
- 16 Length of the fore wings more than 18 mm. Ovipositor shaped as in Fig. 29 *albopunctata*
- Length of the fore wings less than 18 mm. Ovipositor shaped as in Fig. 35 *stricta*
- 17 Seventh abdominal sternite with a single transverse ridge, often more pronounced towards the sides, as in Fig. 20 *sabulosa*
- Seventh abdominal sternite with a central swelling (Figs 21-23) or two transverse ridges (Fig. 24) ...18
- 18 Seventh abdominal sternite with two transverse ridges, as in Fig. 24 *intermedia*
- Seventh abdominal sternite with a central swelling, as in Figs 21-2319
- 19 Subgenital plate with prominent paired protuberances towards the base, as in Fig. 23. Ovipositor more than 2 mm deep at the base of the dark-coloured part *falx*
- Subgenital plate without such protuberances. Ovipositor less than 2 mm deep at the base of the dark-coloured part20
- 20 Subgenital plate with very broad lobes, as in Fig. 22. Ovipositor more strongly curved, as in Fig. 31, usually less than 11.5 mm long *romana*
- Subgenital plate with narrower lobes, as in Fig. 21. Ovipositor more gently curved, as in Fig. 30, usually more than 11.5 mm long *affinis*

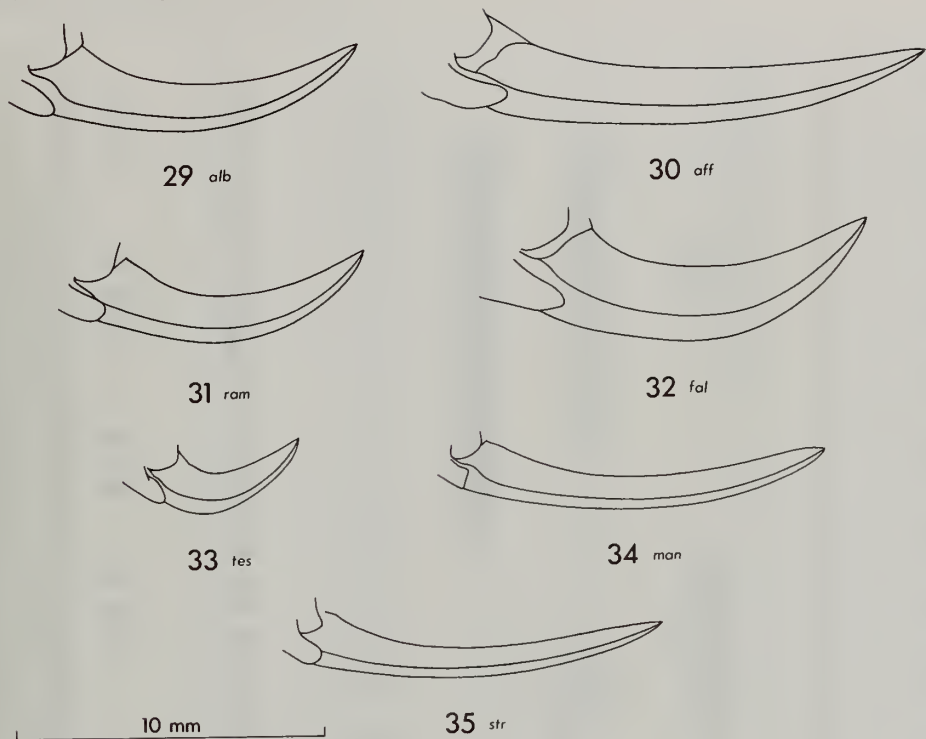
KEY BASED ON SONG CHARACTERS
(see especially Figs 36-48)

The larger species have quite loud songs that are clearly audible in ordinary outdoor conditions to anyone with good high-frequency hearing; for these species the key is based on the calling songs that are produced in warm weather. The four small species, *tessellata*, *veyseli*, *montana* and *stricta*, have songs that are too quiet to be heard in most outdoor situations, and for these species the key is based on the calling songs that are produced by captive males in quiet indoor conditions, especially at night.

Many of the song differences can be detected by careful listening with the human ear assisted by the second hand (or digital count) of a watch, but some of the couplets require oscillographic analysis, or at least the means of playing back a



Figs 18–28 Ventral view of the female terminal abdominal sternites of (18) *Platycleis albopunctata albopunctata*, (19) *P. a. grisea*, (20) *P. sabulosa*, (21) *P. affinis*, (22) *P. romana*, (23) *P. falx*, (24) *P. intermedia*, (25) *P. sepium*, (26) *P. tessellata*, (27) *P. montana*, (28) *P. stricta*.



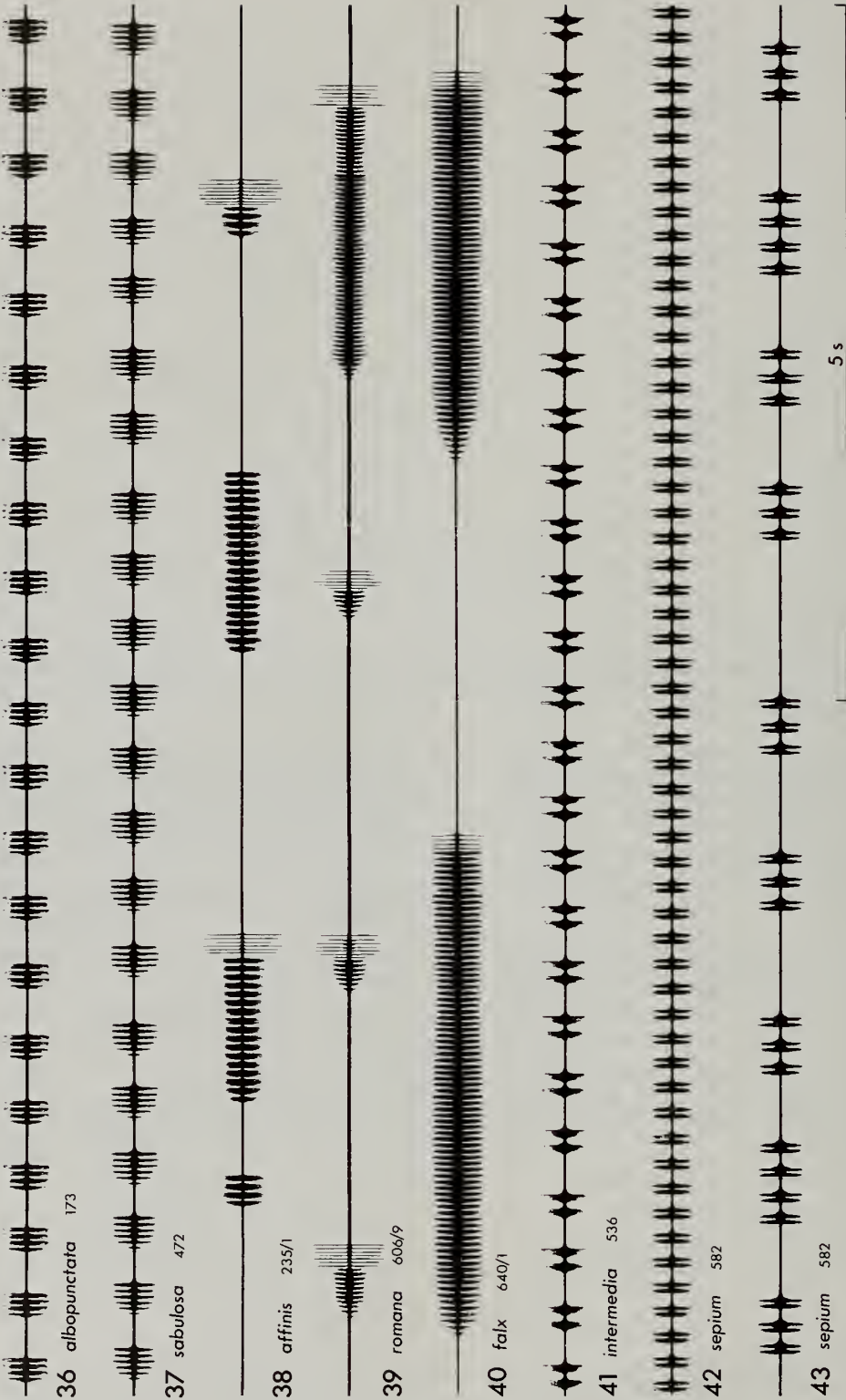
Figs 29–35 Lateral view of the ovipositor of (29) *Platycleis albopunctata*, (30) *P. affinis*, (31) *P. romana*, (32) *P. falx*, (33) *P. tessellata*, (34) *P. montana*, (35) *P. stricta*.

recorded song at a slower tape speed. I have been unable to find a consistent difference between the calling songs of *tessellata* and *veyseli*, but these species are completely allopatric in western Europe and easily separated morphologically.

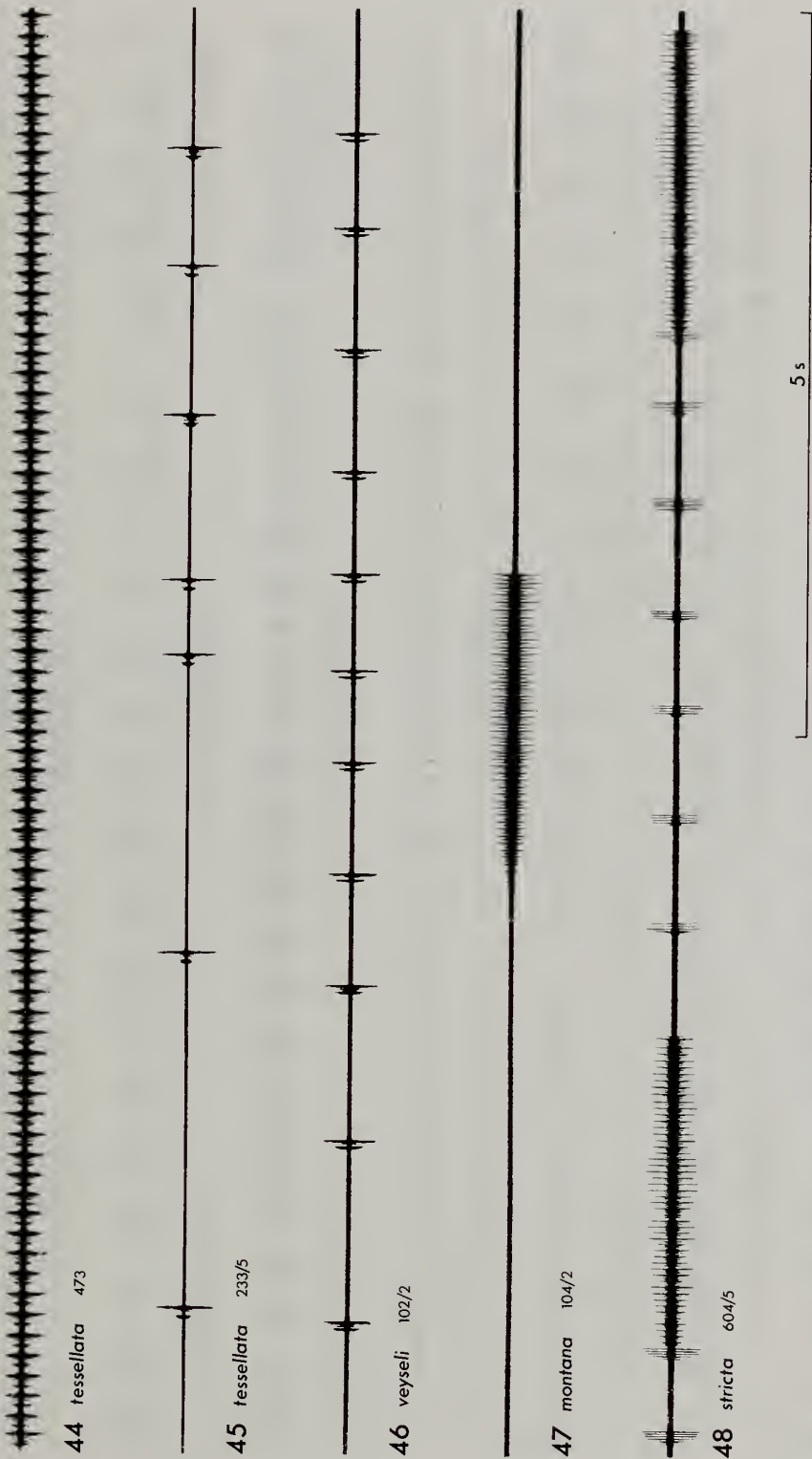
See p. 4 for definitions of the terms ‘echeme’, ‘syllable’, ‘macrosyllable’ and ‘microsyllable’.

- 1 Song consisting of a long series (lasting at least 10 s) of uniformly short echemes or single syllables, in either case lasting less than 0.5 s and repeated regularly at the rate of at least 1/s (Figs 36, 37, 41, 42, 44) 2
- Song consisting of irregularly repeated syllables, or of echemes repeated less frequently than 1/s and at least some lasting more than 0.5 s (Figs 38, 39, 40, 43, 45, 47, 48) 8
- 2 Song consisting of echemes of 2–10 syllables 3
- Song consisting of ungrouped syllables 7
- 3 Echemes composed of a single macrosyllable followed by several microsyllables (Figs 123, 125) ***stricta***
- Echemes composed of 2 or more macrosyllables with no microsyllables 4
- 4 Echemes composed of 2 macrosyllables 5
- Echemes composed of 3 or more macrosyllables ... 6

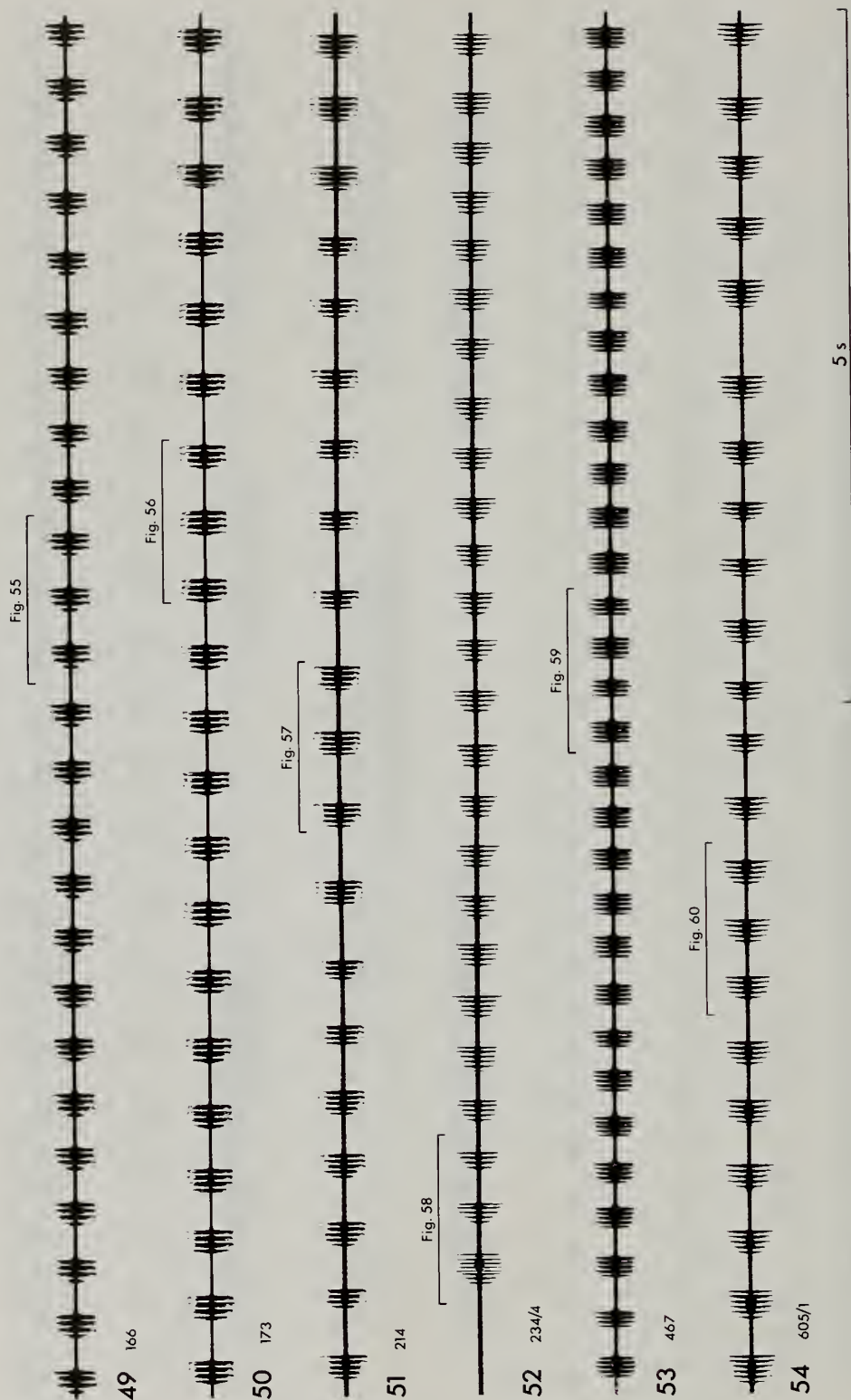
- 5 Echeme repetition rate less than 4/s; syllable repetition rate less than 15/s (Figs 103–105) ... ***intermedia***
- Echeme repetition rate more than 4/s; syllable repetition rate more than 15/s (Figs 99–102) ***sepium***
- 6 Echemes usually composed of 5 or fewer syllables (Figs 49–66) ***albopunctata***
- Echemes usually composed of 6 or more syllables (Figs 67–75) ***sabulosa***
- 7 In western Europe occurring only in eastern Austria ***veyseli***
- Not occurring in Austria ***tessellata***
- 8 Song consisting of disyllabic echemes grouped into short sequences of about 2–4 echemes (Fig. 43) ***sepium***
- Song not consisting of disyllabic echemes 9
- 9 Song consisting of well-separated single syllables repeated irregularly at the rate of less than 7/s ... 10
- Song consisting entirely of echemes; syllable repetition rate more than 7/s 11
- 10 In western Europe occurring only in eastern Austria ***veyseli***
- Not occurring in Austria ***tessellata***



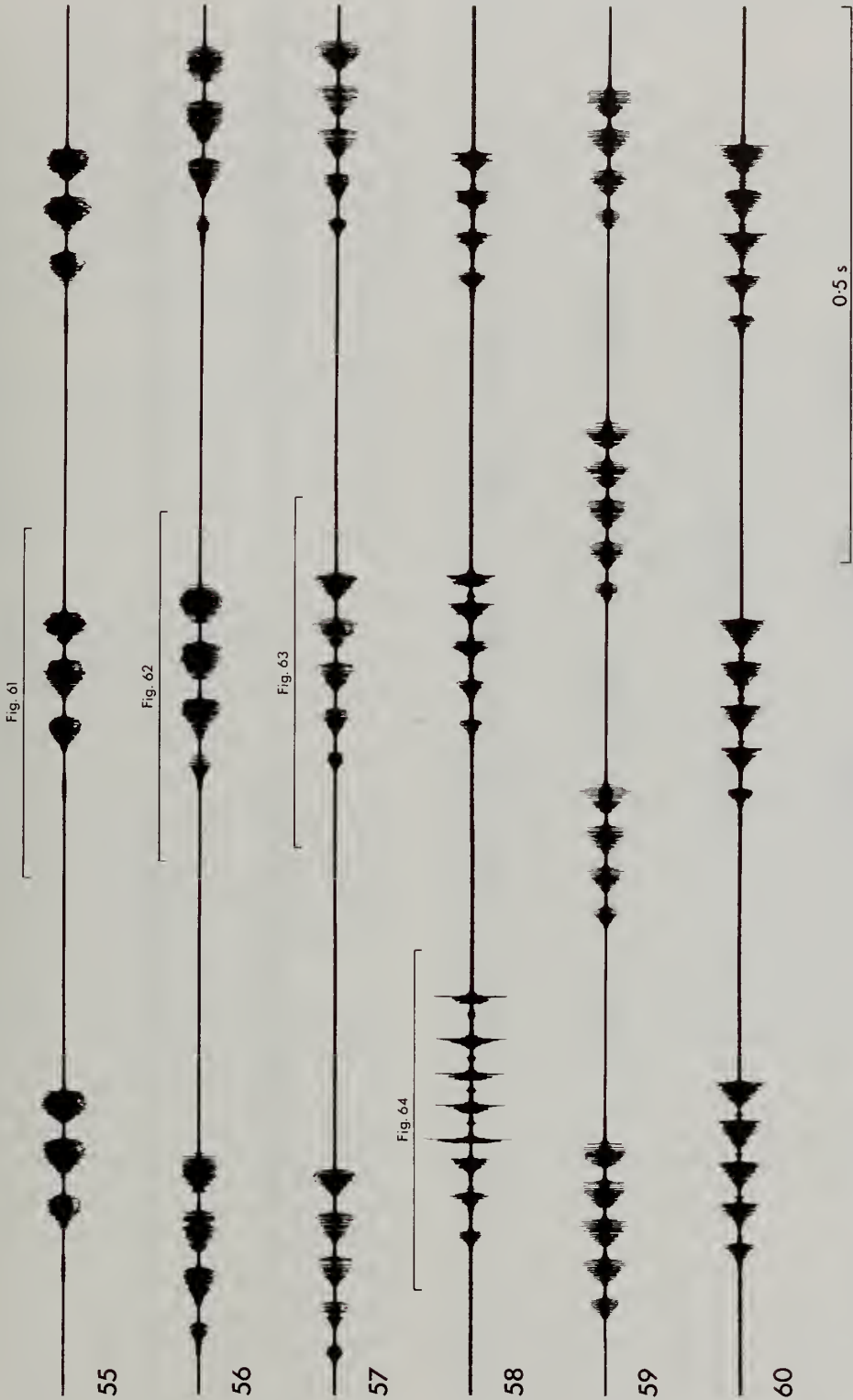
Figs 36–43 Oscillograms of typical male calling songs of species of *Platycleis*. Figs 42 and 43 show the two types of song-pattern produced by males of *P. sepium*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 2, 3).



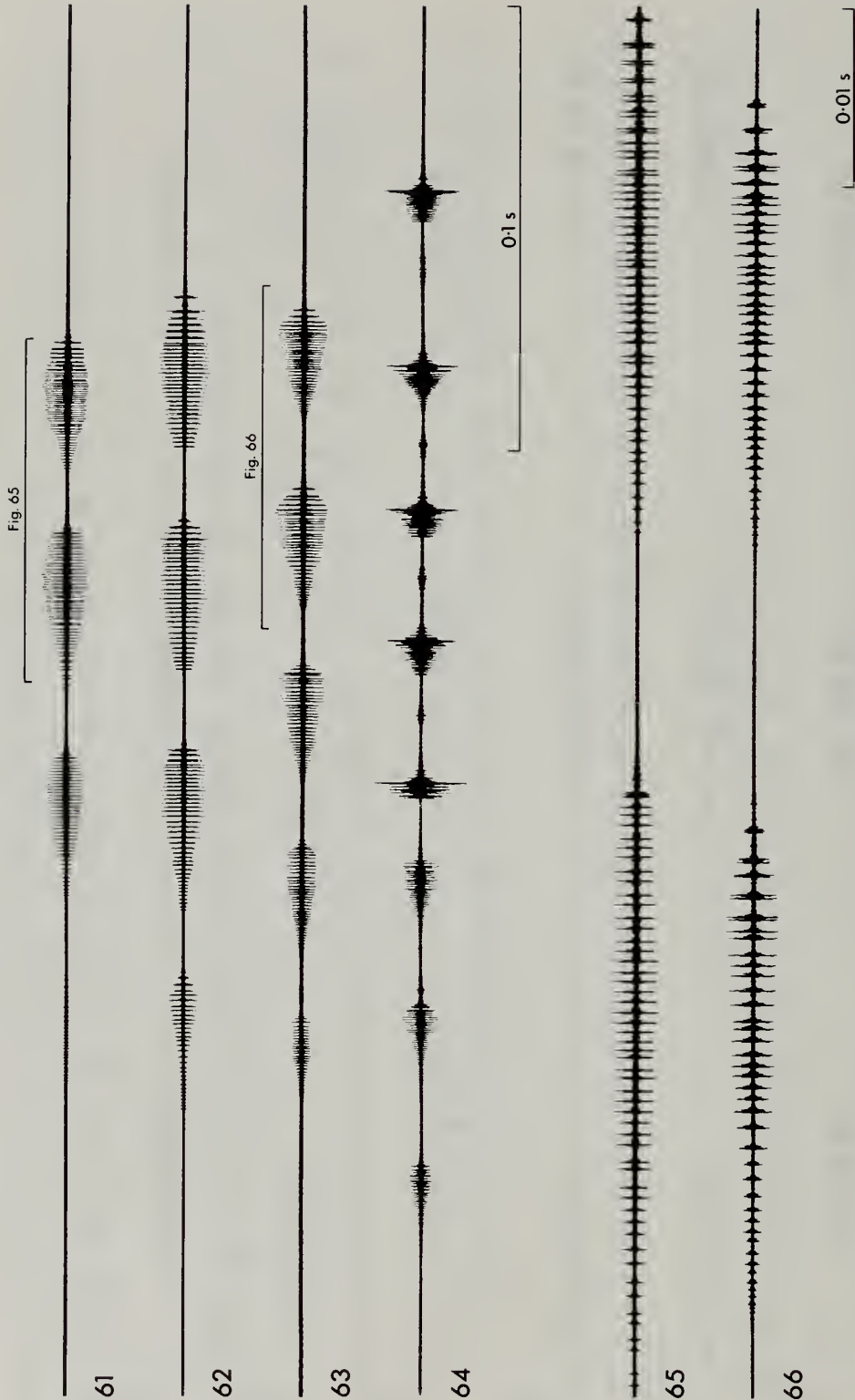
Figs 44–48 Oscillograms of typical male calling songs of species of *Platycleis*. Figs 44 and 45 show the two types of song-pattern produced by males of *P. tessellata*; it is likely that *P. veyseli* also sometimes produces the continuous type of song shown in Fig. 44. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 3).



Figs 49–54 Oscillograms of the callings songs of six males of *Platycleis albopunctata*. Figs 49–53 are from males of *P. a. albopunctata* and Fig. 54 is from a male of *P. a. grisea*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 2, 3).



Figs 55–60 Faster oscillograms of the indicated parts of the songs of *Platycleis albopunctata* shown in Figs 49–54.



Figs 61-66 Faster oscillograms of the indicated parts of the songs of *Platycleis albopunctata* shown in Figs 55-58.

- 11 Song consisting solely of a series of echemes of uniform duration (1–4 s) 12
 - Song consisting of a mixture of short (less than 1 s) and long (1–5 s) echemes 13
- 12 Song consisting of echemes of uniform macrosyllables, often ending with 2–5 microsyllables (Figs 90–98) (Western Mediterranean Region) *false*
 - Song consisting of echemes of alternately quieter and louder macrosyllables without microsyllables (Figs 115–120) (Not known from the western Mediterranean Region) *montana*
- 13 Short echemes consisting of a single macrosyllable followed by several microsyllables (Figs 123, 125) *stricta*
 - Short echemes consisting of more than one macrosyllable, usually followed by several microsyllables 14
- 14 Syllable repetition rate less than 20/s (Figs 76–83) *affinis*
 - Syllable repetition rate more than 20/s (Figs 84–89) *romana*

THE SONGS OF THE WESTERN EUROPEAN *PLATYCLEIS*

Platycleis albopunctata (Goeze)

(Figs 2–4, 18, 19, 29, 49–66)

Gryllus (*Tettigonia*) *albo-punctatus* Goeze, 1778: 89. Based on Roesel, 1749: pl. 20, figs 8–10 (illustrating three different species); Kaltenbach, 1964: 41, in effect designated a lectotype by restricting the application of the name to the species illustrated in fig. 10. No specimens exist and no type locality was specified.

REFERENCES TO SONG. **Oscillogram:** Ahlén, 1981 (as *denticulata*); Broughton, 1965 (as *d.*); Dubrovin & Zhantiev, 1970 (as *intermedia*); Grein, 1984; Heller, 1988; Latimer, 1981b, 1981c; Latimer & Broughton, 1984; Samways, 1976a; Schmidt & Schach, 1978 (as *grisea*). **Diagram:** Bellmann, 1985a; Duijm & Kruseman, 1983; Holst, 1970 (as *d.*); Ragge, 1965 (as *d.*); Samways, 1976c; Wallin, 1979 (as *d.*). **Sonagram:** Samways, 1976a. **Frequency information:** Ahlén, 1981 (as *d.*); Dubrovin & Zhantiev, 1970 (as *i.*); Heller, 1988; Latimer, 1981a, 1981b, 1981c; Latimer & Broughton, 1984; Sales & Pye, 1974. **Musical notation:** Baier, 1930 (as *g.*); Yersin, 1854b (as *g.*). **Verbal description only:** Broughton, 1972; Chopard, 1922; Default, 1987; Faber, 1928 (as *g.*); Harz, 1957 (as *d.*); Sarra, 1934 (as *g.*); Yersin, 1857 (as *g.*). **Disc**

recording: Grein, 1984; Ragge, Burton & Wade, 1965 (as *d.*). **Cassette recording:** Ahlén, 1982 (as *d.*); Bellmann, 1985b; Burton & Ragge, 1987; Wallin, 1979 (as *d.*).

RECOGNITION. Females of this species may be distinguished from other species of similar size by the unmodified seventh abdominal sternite, which has no ridges or other prominences. Males are much more difficult to recognize, but may be distinguished from the closely similar species *sabulosa*, *intermedia*, *affinis* and *false* by the robust titillators, with their rather short apical part and broad basal part (Figs 2–4).

In the field males may be distinguished from most other western European species of *Platycleis* by their calling song, which consists of long sequences of echemes repeated regularly at the rate of about 2–4/s and each usually composed of 3–5 syllables. The calling songs of *sabulosa* and *intermedia* also consist of echemes repeated at similar rates, but each echeme is usually composed of more than 5 syllables in *sabulosa* and of only 2 syllables in *intermedia*. The echemes of *sepium*, which are also disyllabic, are repeated more rapidly than 4/s and are often grouped into short sequences of 2–4 echemes.

SONG. (Figs 49–66). In warm sunshine the calling song consists of long sequences of echemes repeated fairly regularly at the rate of about 2–4/s and each usually consisting of 3–5 (very rarely 2 and occasionally 6) syllables. Oscillographic analysis shows that the opening hemisyllables are often absent and that the closing hemisyllables usually last about 10–30 ms and are repeated within an echeme at the rate of about 25–35/s. The duration of a single echeme of four syllables is about 100–200 ms and the interval between two echemes is about 100–300 ms. In dull weather and at night the echeme repetition rate can drop to less than 1/s and the syllable repetition rate to less than 10/s; in such conditions the closing hemisyllables sometimes last more than 100 ms and a four-syllable echeme more than 600 ms. The first syllable in an echeme is usually quieter than the remaining ones. Microsyllables are usually absent, but occasionally a few are added at the end of an echeme, especially the opening echeme of a sequence (see Figs 52, 58, 64).

DISTRIBUTION. This species occurs very widely in Europe from southern Scandinavia to the southern peninsulas, where it is mainly confined to uplands. It is also recorded from mountains in Morocco. Further song studies are needed to establish the eastern limit of the range of *albo-punctata*. The species can be divided broadly into

two subspecies (see p. 7) on the basis of small morphological differences, mainly the shape of the male titillators (Figs 2–4) and female subgenital plate (Figs 18, 19); there is no difference in the calling song. The nominate subspecies occurs in the westernmost parts of Europe (including Scandinavia, West Germany, southern Britain, France and the Iberian Peninsula) and the eastern subspecies, *P. a. grisea* (Fabricius), from Poland, Czechoslovakia, Austria and Italy eastwards. In parts of East Germany and the Alps transitional forms occur.

Platycleis sabulosa Azam

(Figs 5, 10, 20, 67–75)

Platycleis sabulosa Azam, 1901: 157. Syntypes of both sexes, FRANCE: Fréjus (MNHN, Paris) [putative syntypes examined].

REFERENCES TO SONG. **Oscillogram:** Heller, 1988; Latimer & Broughton, 1984; Samways, 1976a. **Diagram:** Samways, 1976c. **Sonagram:** Samways, 1976a. **Verbal description only:** Defaut, 1987.

RECOGNITION. Females of this species are characterized by the seventh abdominal sternite, which has a pair of lateral protuberances (often connected so as to form a transverse ridge) (Fig. 20). Males are difficult to recognize morphologically, but may be distinguished from *albopunctata* by the shape of the titillators (cf. Figs 2–4, 5) and from *intermedia* and *affinis* by the shape of the tenth abdominal tergite (Fig. 10). Both sexes have a shorter pronotum than *falx* (usually less than 6.5 mm in the male, 7.0 mm in the female; usually more than these values in *falx*).

In the field males may be distinguished from most other western European members of the genus by their calling song, consisting of long sequences of echemes repeated regularly at the rate of about 1–3/s and each usually composed of 6–7 syllables. The calling song of *albopunctata* is quite similar, but its echemes rarely contain more than 5 syllables.

SONG. (Figs 67–75). The calling song consists of long sequences of echemes repeated fairly regularly at the rate of about 1–3/s and each usually consisting of 6–7 (occasionally 5 and rarely up to 10) syllables. Oscillographic analysis shows that the opening hemisyllables are often absent and that the closing hemisyllables usually last about 10–40 ms and are repeated within an echeme at the rate of about 20–40/s. The duration of a single echeme of six syllables is usually about 150–300 ms and the interval between two echemes about 150–500 ms. In dull weather and at night the

repetition rates are decreased and the duration of the syllables and echemes increased. The first syllable in an echeme is usually quieter than the remaining ones and the syllables sometimes become steadily louder through most of the echeme. Microsyllables are usually absent.

DISTRIBUTION. The Mediterranean coast of France, the Iberian Peninsula, Morocco and Algeria; also recorded from Sicily, the Canary Islands and Israel.

Platycleis affinis Fieber

(Figs 6, 11, 17, 21, 30, 76–83)

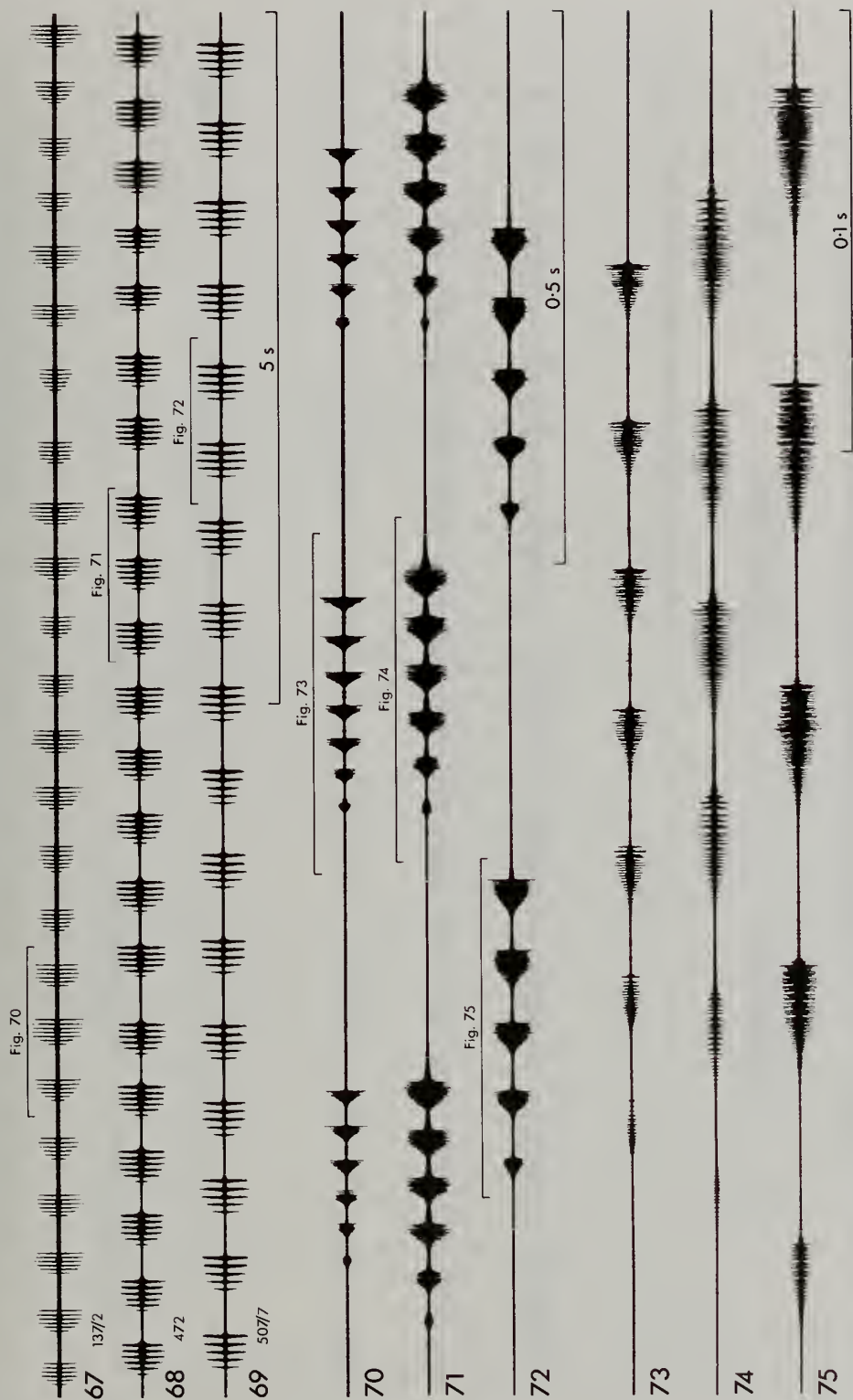
Platycleis affinis Fieber, 1853: 150. Type(s), SOUTHERN EUROPE (lost).

REFERENCES TO SONG. **Oscillogram:** Broughton, 1955, 1965; Heller, 1988; Latimer & Broughton, 1984; Samways, 1976a, 1976b; Schmidt & Schach, 1978. **Diagram:** Broughton & Lewis, 1979; Samways, 1976c. **Sonagram:** Broughton, Samways & Lewis, 1975; Samways, 1976a. **Frequency information:** Heller, 1988; Latimer & Broughton, 1984. **Verbal description only:** Defaut, 1987.

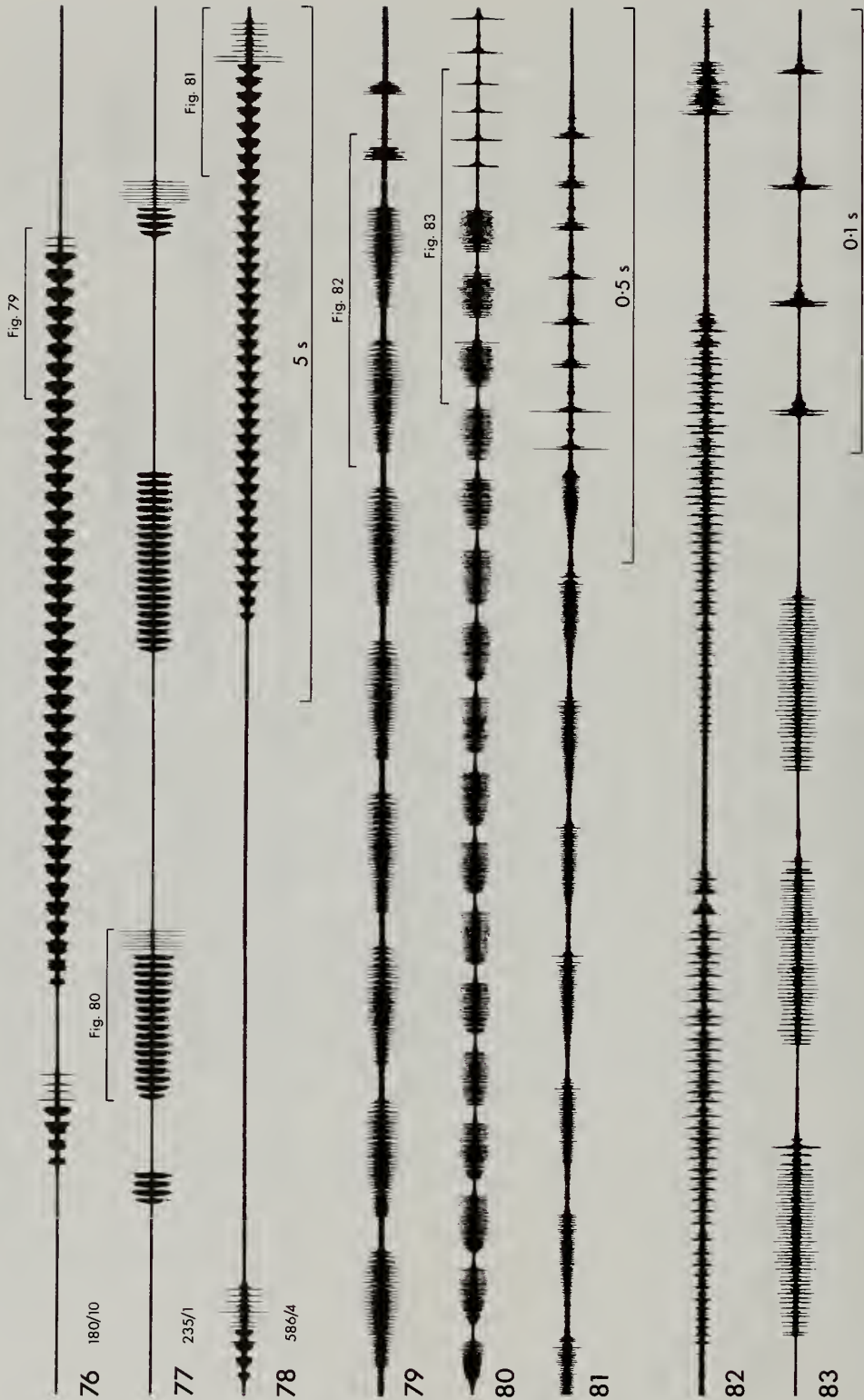
RECOGNITION. Females of this species may be recognized by the seventh abdominal sternite, which has a large median protuberance (Fig. 21); there is a similar protuberance in *falx*, but in that species the ovipositor is shorter and deeper than in *affinis* (cf. Figs 30, 32) and the subgenital plate has a paired prominence towards the base. Males may be distinguished from *albopunctata* by the shape of the titillators (cf. Figs 2–4, 6), from *sabulosa* and *falx* by the shape of the tenth abdominal tergite (cf. Figs 10, 11, 13) and (usually) from *intermedia* by the conspicuously pale-coloured basal part of *M* in the fore wings.

In the field males may be recognized by the calling song, which consists of a mixture of short (less than 1 s) and long (1–5 s) echemes, mostly ending with microsyllables and with a syllable repetition rate of less than 20/s.

SONG. (Figs 76–83). The calling song consists of a mixture of short echemes lasting less than 1 s and usually composed of fewer than 7 macrosyllables, and longer echemes lasting 1–5 s and composed of 8–50 macrosyllables. Each echeme usually ends with a series of 2–9 microsyllables. The echemes are often grouped into one or two short ones followed by a long one, but sometimes they follow one another quite irregularly and occasionally there is a fairly regular sequence of long echemes with few short ones. Oscillographic analysis shows that the opening hemisyllables are usually absent



Figs 67-75 Oscillograms at three different speeds of the calling songs of *Platycleis sabulosa*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 2, 3).



Figs 76-83 Oscillograms at three different speeds of the calling songs of three males of *Playcteis affinis*. Fig. 77 is from a typical daytime song in sunny weather; Figs 76 and 78 are from night-time recordings and show the slower rhythm resulting from lower body temperatures. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 2, 3).

and that the closing macrosyllables usually last about 30–110 ms and are repeated at the rate of about 10–20/s. The microsyllables usually last about 3–15 ms and are repeated at the rate of about 17–45/s; the microsyllable sequence at the end of an echeme seldom lasts more than 0.3 s. The echemes often begin quietly and the first one or two syllables are often shorter than the remaining ones. The intervals between echemes vary greatly: long echemes often follow short echemes with an interval of less than a second or with no pause at all; intervals of a few seconds are common and sometimes there are longer intervals of 30 s or more.

DISTRIBUTION. Like *intermedia* this species occurs in a large part of the Mediterranean Region, including Morocco and Algeria. Its range extends eastwards to Turkey and southern Asia, and in central Europe it occurs a little further north than *intermedia* in Lower Austria and Hungary.

Platycleis romana Ramme

(Figs 7, 12, 22, 31, 84–89)

Platycleis romana Ramme, 1927: 142. Holotype ♀, ITALY: Lazio, Albany Hills, between Castel Gandolfo and Rocca di Papa, 9.vii.1924 [not '9.III.1926', as stated by Ramme] (W. Ramme) (MNHU, Berlin) [examined].

REFERENCES TO SONG. The only original published reference to the song known to me is a very brief mention by Ingrisch (1981: 91) that the song is reminiscent of *affinis*.

RECOGNITION. Females of this species may be recognized by the subgenital plate, which has unusually broad lobes with a fairly narrow median groove (Fig. 22); the seventh abdominal sternite lacks the large protuberance shown by *affinis* and *falx*, but is swollen in the anterior part (Fig. 22). Males may be distinguished from Italian *albopunctata*, *affinis* and *intermedia* by the shape of the titillators (cf. Figs 2–4, 6, 7, 9), and from *sabulosa* and *falx* by the shape of the tenth abdominal tergite (cf. Figs 10, 12, 13).

In the field males may be recognized by the calling song, which consists of a mixture of short and long echemes, each usually ending with microsyllables. The song is thus similar to that of *affinis*, but the syllable repetition rate is much higher, more than 20/s.

SONG. (Figs 84–89). The calling song consists of a mixture of short echemes usually lasting less than 0.5 s and composed of fewer than 10 macrosyllables, and longer echemes lasting up to 3 s and

composed of 15–80 macrosyllables. Each echeme usually ends with a series of up to 10 microsyllables. Oscillographic analysis shows that quiet opening hemisyllables are often present; the closing macrosyllables last about 20–30 ms and are repeated at the rate of about 25–40/s. The closing microsyllables last about 2–3 ms and are repeated at the rate of about 35–50/s; the microsyllable sequence at the end of an echeme usually lasts less than 0.3 s. The echemes usually begin quietly and the first one or two syllables are often shorter than the remaining ones. The intervals between echemes vary from less than 1 s to more than 4 s.

DISTRIBUTION. Known only from Italy, where it is quite widespread.

Platycleis falx (Fabricius)

(Figs 8, 13, 23, 32, 90–98)

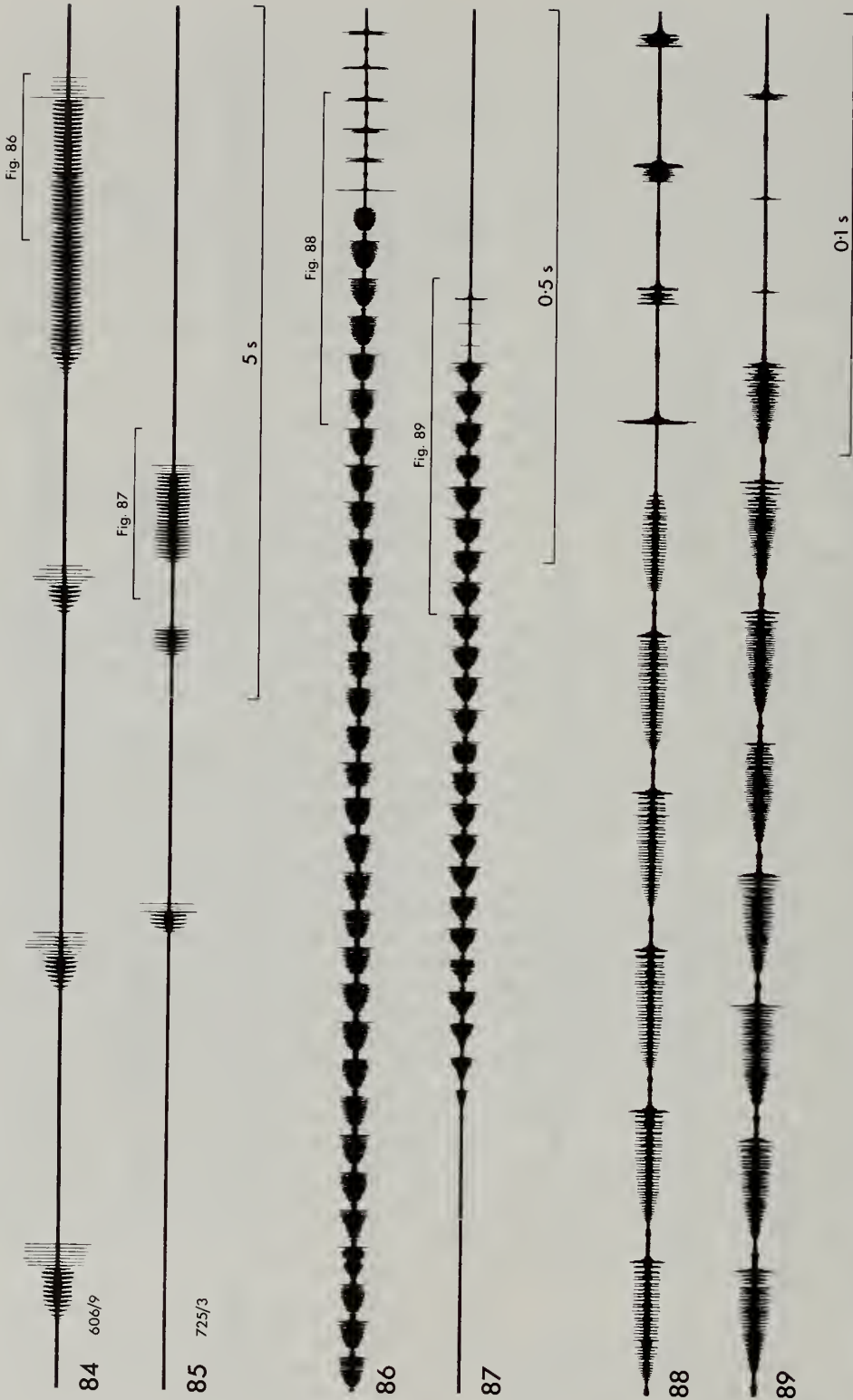
Locusta falx Fabricius, 1775: 286. Lectotype ♀, MADEIRA (BMNH), designated by Uvarov (1930: 402) [examined].

REFERENCES TO SONG. **Oscillogram:** Heller, 1988; Samways, 1976a. **Diagram:** Samways, 1976c. **Sonagram:** Samways, 1976a. **Frequency information:** Busnel, 1955; Heller, 1988. **Verbal description only:** Yersin, 1857 (as *intermedius*).

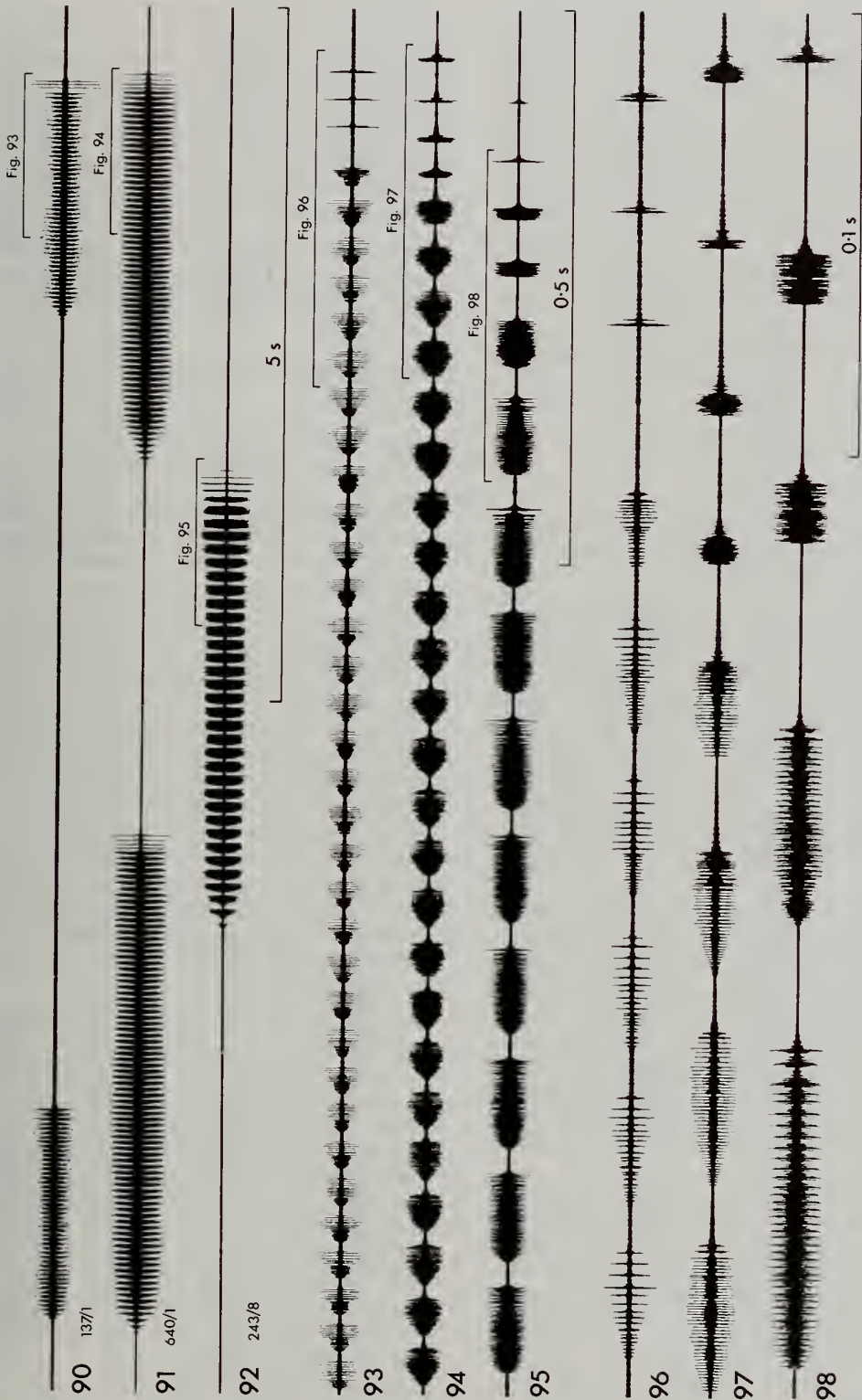
RECOGNITION. Females of this species may be recognized by the paired prominence towards the base of the subgenital plate (Fig. 23), and the large median protuberance on the seventh abdominal sternite (Fig. 23); there is a similar protuberance in *affinis*, but in that species the ovipositor is longer and less deep than in *falx* (cf. Figs 30, 32). Males may be distinguished from *albopunctata* by the shape of the titillators (cf. Figs 2–4, 8), and from *affinis* and *intermedia* by the shape of the tenth abdominal tergite (cf. Figs 11, 13, 14). Both sexes have a longer pronotum than *sabulosa* (usually more than 6.5 mm in the male, 7.0 in the female; usually less than these values in *sabulosa*).

In the field males may be recognized by the calling song, which consists of long sequences of echemes, each usually lasting 1–4 s and often ending with microsyllables. The echemes are fairly uniform in duration within one song (in contrast to the short and long echemes of *affinis* and *romana*) and are usually separated by intervals of about 4–10 s.

SONG. (Figs 90–98). The calling song consists of a long sequence of echemes, each usually lasting 1–4 s, composed of about 25–90 macrosyllables and often ending with about 2–5 microsyllables. Within one song the echemes are usually fairly



Figs 84–89 Oscillograms at three different speeds of the calling songs of two males of *Playcycleis romana*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 2).



Figs 90–98 Oscillograms at three different speeds of the calling songs of three males of *Platycleis falx*. Figs 90 and 91 are from typical daytime songs in sunny weather; Fig. 92 is from a night-time recording and shows the slower rhythm resulting from a lower body temperature. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 2).

uniform in duration and are usually separated by intervals of about 4–10 s. Oscillographic analysis shows that the opening hemisyllables are usually absent and that the closing macrosyllables usually last about 20–85 ms and are repeated at the rate of about 10–30/s. The microsyllables usually last about 1–12 ms and are repeated at the rate of about 20–40/s; the microsyllable sequence at the end of an echeme seldom lasts more than 0.2 s. The echemes usually begin quietly, reaching maximum intensity by the third to seventh syllable, and the first one or two syllables are usually shorter than the remaining ones.

DISTRIBUTION. Found on Madeira and in the western Mediterranean Region from Spain and Morocco to the Italian Peninsula and Tunisia.

Platycleis intermedia (Serville)

(Figs 9, 14, 24, 103–105)

Decticus intermedius Serville, [1838]: 488. Syn-types of both sexes, FRANCE: Montpellier and Château-Gombert (lost).

REFERENCES TO SONG. **Oscillogram:** Broughton, 1965 (as *sabulosa*), Elsner & Popov, 1978; Heller, 1988; Latimer & Broughton, 1984; Lewis, 1974; Messina *et al.*, 1980; Samways, 1976a, 1976b. **Diagram:** Broughton & Lewis, 1979; Samways, 1976a, 1976c. **Sonagram:** Broughton, Samways & Lewis, 1975; Samways, 1976a. **Frequency information:** Heller, 1988; Lewis, Seymour & Broughton, 1975; Zhantiev & Dubrovin, 1971. **Verbal description only:** Chopard, 1952; Pinedo, 1985.

RECOGNITION. Females of *intermedia* may be recognized by the seventh abdominal sternite, which has two prominences, one near the middle and one near the posterior margin (Fig. 24), both variable in shape and size. Males may be distinguished from *albopunctata* by the shape of the titillators (cf. Figs 2–4, 9), from *sabulosa* and *falx* by the shape of the tenth abdominal tergite (cf. Figs 10, 13, 14) and (usually) from *affinis* by the inconspicuously coloured basal part of *M* in the fore wings.

In the field males may be recognized by the calling song (produced mainly in the evening and at night), which consists of long sequences of disyllabic echemes repeated at the rate of 2–3/s. The echemes of *sepium* are also disyllabic, but are repeated more rapidly than 4/s and are often grouped into short sequences of 2–4 echemes.

SONG. (Figs 103–105). The calling song, produced mainly in the evening and at night, consists of long

sequences of disyllabic echemes repeated fairly regularly at the rate of about 2–3/s. Oscillographic analysis shows that the opening hemisyllables are usually absent and that the closing hemisyllables usually last about 40–90 ms, the second of each pair often being a little longer, and sometimes louder, than the first. The duration of each echeme is about 130–180 ms and the interval between two echemes is about 140–250 ms. Microsyllables are usually absent.

DISTRIBUTION. Found in a large part of the Mediterranean Region, from Spain and Morocco to Turkey and further east into southern Asia.

Platycleis sepium (Yersin)

(Figs 25, 99–102)

Decticus sepium Yersin, 1854a: 68. 3 ♂, 2 ♀ syntypes, FRANCE: Nice (lost).

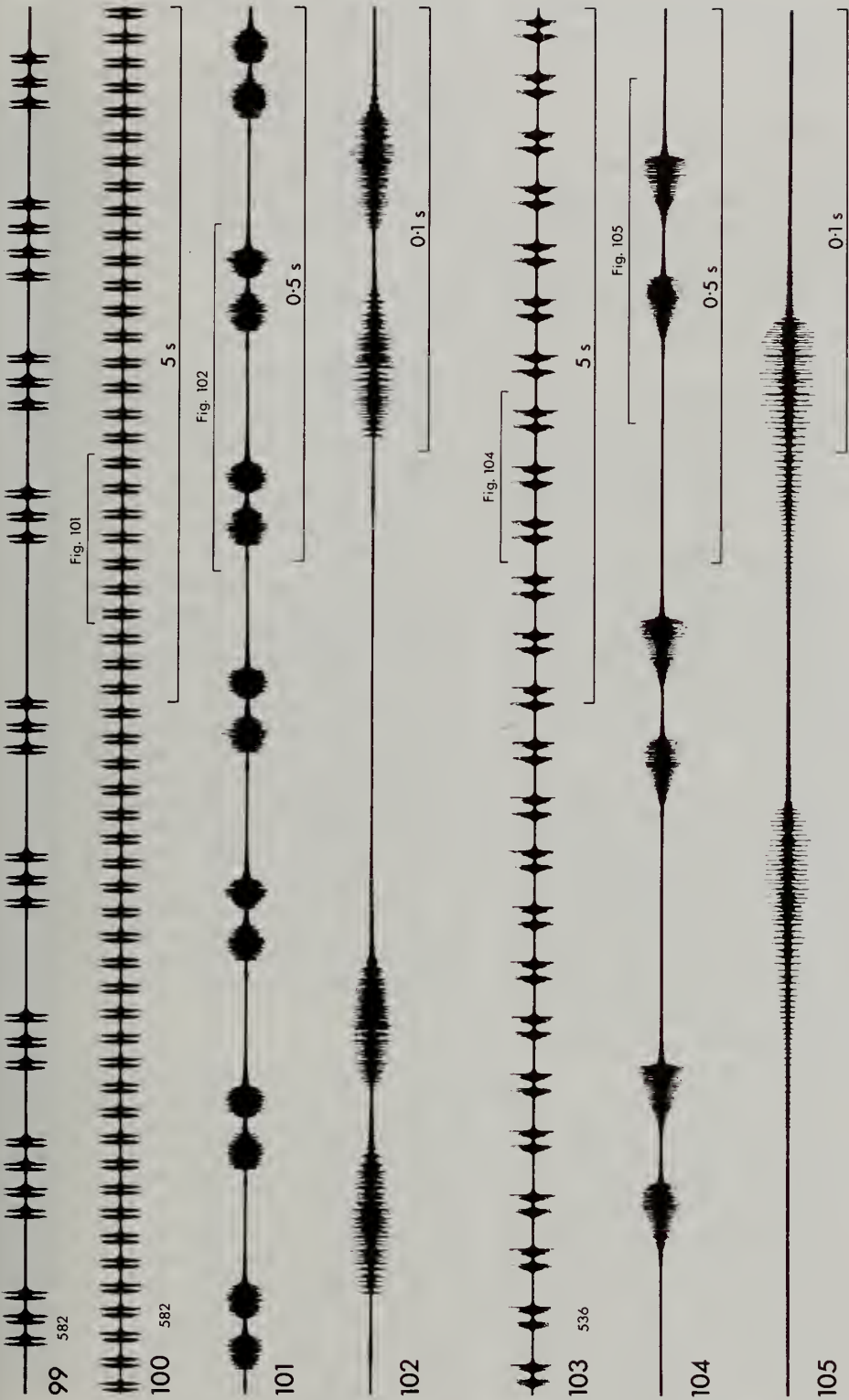
REFERENCES TO SONG. **Oscillogram:** Dubrovin & Zhantiev, 1970; Heller, 1988. **Frequency information:** Heller, 1988. **Musical notation:** Yersin, 1854b. **Verbal description only:** Chopard, 1922.

RECOGNITION. This species differs from all other western European species of *Platycleis* of comparable size in being brachypterous, the fore wings not reaching the tip of the abdomen. Females are also well characterized by the terminal abdominal sternites: both the sixth and seventh sternites have a bifid prominence and the subgenital plate is uniquely shaped (Fig. 25).

In the field males may be recognized by the calling song, which consists of disyllabic echemes repeated at the rate of more than 4/s and often grouped into short sequences of 2–4 echemes. The echemes of *intermedia* are also disyllabic, but are repeated less frequently than 4/s and are usually in long ungrouped sequences.

SONG. (Figs 99–102). The calling song consists of disyllabic echemes repeated at the rate of about 4–15/s, often grouped into short sequences of 2–4 echemes (Fig. 99) but sometimes in long sequences of indefinite duration (Fig. 100). Oscillographic analysis shows that the opening hemisyllables are often present (though always very quiet) and that the closing hemisyllables usually last about 10–50 ms. The duration of each echeme (excluding the first opening hemisyllable, when present) is about 45–100 ms and the intervals between the echemes (within a group or during long sequences) are usually about 60–130 ms. There are no microsyllables.

DISTRIBUTION. This species occurs in southern Europe from the Mediterranean coast of France



Figs 99–105 Oscillograms at three different speeds of the male calling song of (99–102) *Platycleis sepium* and (103–105) *P. intermedia*. Figs 99 and 100 were taken from the same male and show the two types of song-pattern produced by *P. sepium*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 3).

to the extreme south of European U.S.S.R., including the Italian and Balkan Peninsulas and Asia Minor. From Iberia there are only old records from Catalonia.

Platycleis tessellata (Charpentier)

(Figs 26, 33, 106, 107, 109, 110, 112, 113)

Locusta tessellata Charpentier, 1825: 121. Unknown number of syntypes, FRANCE: south, and PORTUGAL: 'Lusitania' (lost).

Platycleis (*Tessellana*) *holoptera emrahi* Koçak, 1984: 169. [Unnecessary replacement name for *Locusta tessellata* Charpentier (see p. 6).] **Syn. n.**

REFERENCES TO SONG. **Oscillogram:** Grein, 1984; Heller, 1988. **Diagram:** Duijm & Kruseman, 1983. **Frequency information:** Heller, 1988; Latimer & Broughton, 1984. **Verbal description only:** Chopard, 1922; Rentz, 1963. **Disc recording:** Grein, 1984.

RECOGNITION. Among the small western European species of *Platycleis*, *tessellata* may be distinguished from *montana* and *stricta* by the short, strongly curved ovipositor (Fig. 33) and modified seventh abdominal sternite (Fig. 26) of the female, and the male cerci, of which the inner tooth is nearer the tip than the base. Both sexes may be distinguished from *veyseli* by the fully developed wings.

Live males in captivity may be distinguished from all other species of *Platycleis* with overlapping distributions by the calling song, which consists of a series of quiet diplosyllables, sometimes repeated regularly at the rate of about 6–8/s but at other times less frequently and more irregularly. The calling song of *veyseli* seems to be identical, but as that species is absent from the whole of western Europe (qualifying for inclusion here only because of its occurrence in the extreme east of Austria) confusion between the songs of these two species is unlikely.

SONG. (Figs 106, 107, 109, 110, 112, 113). The calling song consists of a series of quiet diplosyllables, each lasting about 80–200 ms and composed of an opening hemisyllable lasting about 12–50 ms and a closing hemisyllable lasting about 30–130 ms. The syllables are sometimes repeated regularly at the rate of about 6–8/s for long periods of a minute or more (Fig. 106), but at other times they are repeated much less frequently (about 1–4/s) and less regularly (Fig. 107). Sometimes they are grouped into rather loose echemes of very variable duration. The intervals between syllables vary from about 30–100 ms when they

are repeated regularly to about 0.1–1.0 s or more when the repetition rate is irregular. There are no microsyllables.

DISTRIBUTION. Widespread in the western Mediterranean Region (including North Africa), extending northwards to central France and southern Germany, and eastwards to southern U.S.S.R. and Asia Minor, but not occurring in Austria or the southern part of the Balkan Peninsula. Introduced into California, U.S.A.

Platycleis veysseli Koçak

(Figs 108, 111, 114)

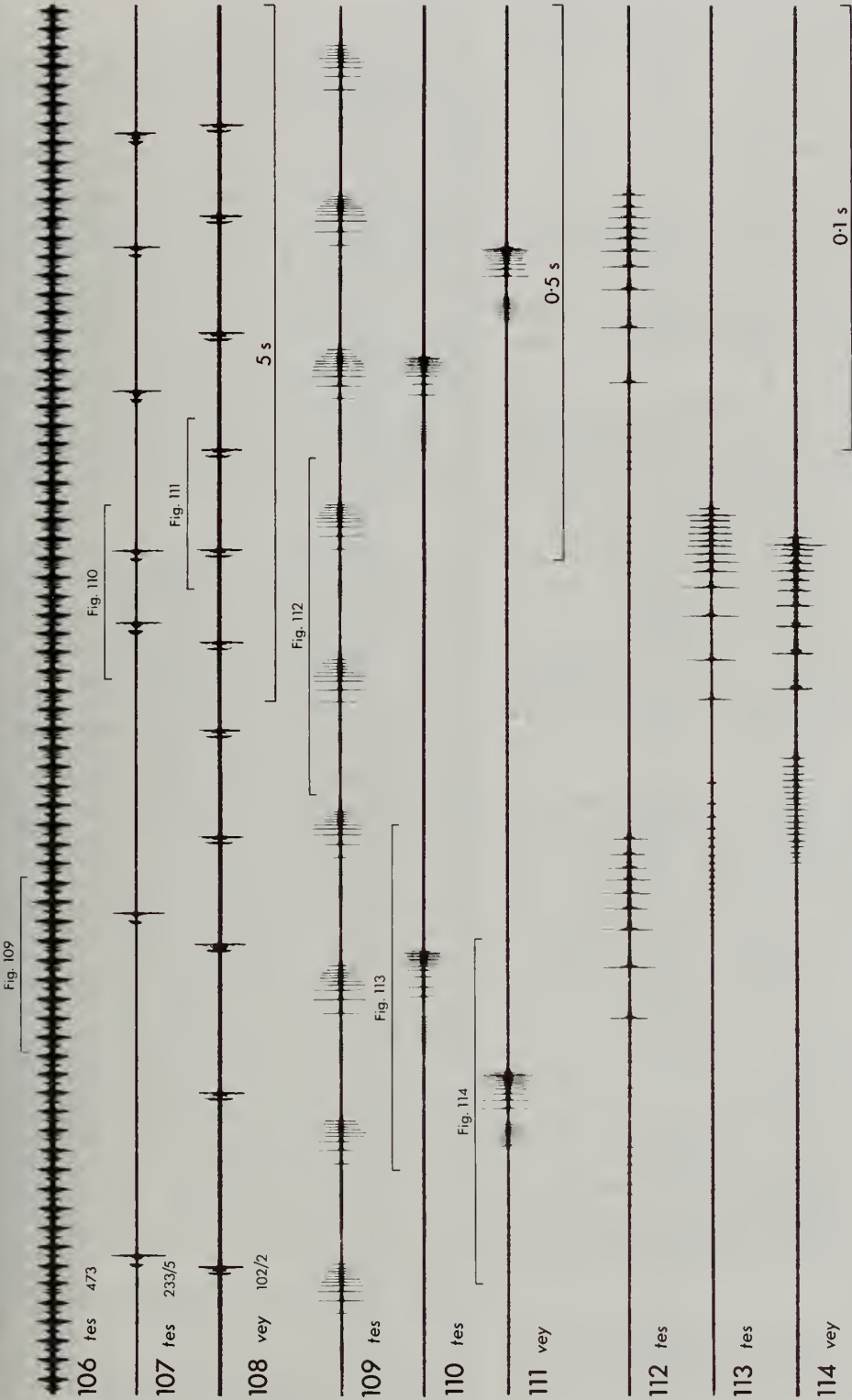
Locusta vittata Charpentier, 1825: 115. Type(s), HUNGARY (lost) [one female putative type specimen in MNHU, Berlin examined]. [Primary homonym of *Locusta vittata* Thunberg, 1789: 102.]

Platycleis (*Tessellana*) *veyseli* Koçak, 1984: 169. [Replacement name for *Locusta vittata* Charpentier.]

REFERENCES TO SONG. **Oscillogram:** Heller, 1988 (as *vittata*); Schmidt & Schach, 1978 (as *vit.*). **Frequency information:** Heller, 1988 (as *vit.*). **Verbal description only:** Harz, 1962 (as *vit.*).

RECOGNITION. This species may be distinguished from the other small species of *Platycleis* occurring in western Europe by its reduced wings, the fore wings not reaching the tip of the abdomen and the hind wings not reaching the tips of the fore wings. The calling song, consisting of a series of quiet diplosyllables, enables live males in captivity to be distinguished from all other species of *Platycleis* with overlapping distributions. The calling song of *tessellata* seems to be identical, but confusion is unlikely in practice as the distributions of the two species do not overlap in western Europe.

SONG. (Figs 108, 111, 114). The calling song consists of a series of quiet diplosyllables, each lasting about 60–80 ms and composed of an opening hemisyllable lasting about 20–25 ms and a closing hemisyllable lasting about 25–35 ms. In the song of the single male studied (in dim light at an air temperature of 26°C) the syllables were grouped into loose echemes of 7–16 syllables, during which the syllable repetition rate averaged about 1/s and the syllables were separated by intervals of about 0.4–1.6 s. It is likely that the study of further males under varying conditions would show that the song varies in the same way as that of *tessellata* (p. 000). There are no microsyllables.



Figs 106–114 Oscillograms at three different speeds of the male calling song of (106, 107, 109, 110, 112, 113) *Platycleis tessellata* and (108, 111, 114) *P. veysseli*. Figs 106 and 107 show the two types of song-pattern produced by *P. tessellata*; it is likely that *P. veysseli* also sometimes produces the continuous type of song shown in Fig. 106. The small numbers following the name abbreviations refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 3).

DISTRIBUTION. In the area studied *veyseli* occurs only in the extreme east of Austria; elsewhere its range extends through south-east Europe (but not the southern part of the Balkan Peninsula) to southern U.S.S.R. and Iran.

***Platycleis montana* (Kollar)**

(Figs 15, 27, 34, 115–120)

Locusta montana Kollar, 1833: 79. Holotype ♀, AUSTRIA: near Vienna, Mödling (NM, Vienna) [examined].

REFERENCES TO SONG. **Oscillogram:** Heller, 1988. **Diagram:** Bellmann, 1985a. **Cassette recording:** Bellmann, 1985b.

RECOGNITION. This species may be distinguished from *tessellata* and *veyseli* by the long, gently curved ovipositor (Fig. 34) and unmodified seventh abdominal sternite of the female, and the male cerci, of which the inner tooth is nearer the base than the tip. Females may be distinguished from the related species *stricta* by the truncate subgenital plate (Fig. 27) and males by the shape of the tenth abdominal tergite (Fig. 15).

Live males in captivity may be recognized by the calling song, which consists of a series of quiet echemes, each lasting about 1–2 s, sometimes repeated regularly at the rate of one every 3–4 s but at other times less frequently and more irregularly.

SONG. (Figs 115–120). The calling song consists of a series of quiet echemes, each lasting about 1–2 s, sometimes repeated regularly at the rate of one every 3–4 s but at other times less frequently and more irregularly. Oscillographic analysis shows each echeme to consist of about 60–140 alternately quieter and louder closing hemisyllables following one another at the rate of about 40–70/s. The quieter closing hemisyllables last about 4–11 ms and the louder ones about 7–17 ms; opening hemisyllables, always quieter than the closing hemisyllables, are often also present. The echemes are usually quieter at the beginning, reaching maximum intensity after about 10–20 syllables. Sometimes the echemes end in a series of loud closing syllables without the interposition of quieter ones (Figs 118, 120), and occasionally there are two quieter closing hemisyllables between two consecutive louder ones. There are no microsyllables.

DISTRIBUTION. This primarily eastern European species occurs in Germany (very locally), eastern Austria, Yugoslavia, Hungary and eastwards to central Asia.

***Platycleis stricta* (Zeller)**

(Figs 16, 28, 35, 121–125)

Decticus strictus Zeller, 1849: 116. Holotype ♀, ITALY: near Rome, Via Appia (NM, Vienna) [examined].

REFERENCES TO SONG. **Oscillogram:** Heller, 1988.

RECOGNITION. Like *montana*, this species may be distinguished from *tessellata* and *veyseli* by the long, gently curved ovipositor (Fig. 35) and unmodified seventh abdominal sternite of the female, and the male cerci, of which the inner tooth is nearer the base than the tip. Females may be distinguished from *montana* by the bilobed subgenital plate (Fig. 28), and males by the shape of the tenth abdominal tergite (Fig. 16).

A stationary live male in captivity may be recognized by the calling song, which consists of a long series of short echemes interspersed with much longer ones.

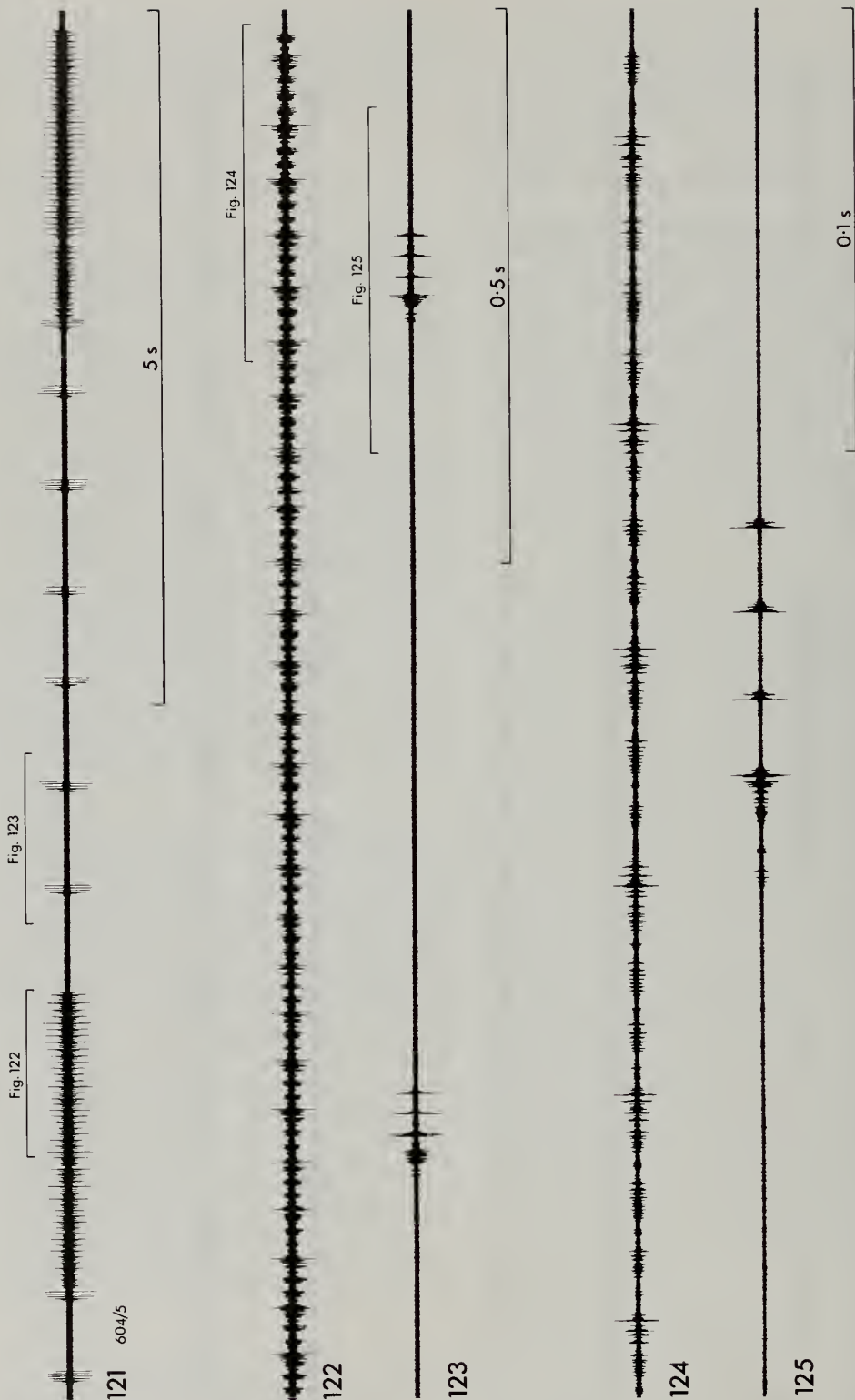
SONG. (Figs 121–125). The fully developed calling song from a stationary male consists of short echemes interspersed with much longer ones and often continues for several minutes. There are about 4–7 short echemes, repeated at intervals of about 0.3–1.2 s, between successive longer echemes; the short echemes last about 50–100 ms and the longer ones about 1–2 s. Oscillographic analysis shows that the short echemes consist of a macrosyllable lasting about 20–30 ms followed by a series of about 3–4 microsyllables, each lasting about 1–5 ms and repeated at the rate of about 50–55/s. The longer echemes follow immediately after a short echeme of this type and consist of a dense sequence of about 90–170 macrosyllables repeated at the rate of about 60–90/s. The syllables in these larger echemes are in groups of three (occasionally four) in which the first one is the quietest and shortest (lasting about 8–12 ms) and the last one the loudest and longest (lasting about 15–20 ms); each group lasts about 40–45 ms and the groups follow one another without any intervening pauses. Opening hemisyllables, always quieter than the closing hemisyllables, are usually present in both the shorter and longer echemes (and are included in the syllable durations given above). There are often small groups of microsyllables interrupting the regular flow of the longer echemes.

While singing males are moving they generally produce only the short echemes.

DISTRIBUTION. Widespread in Italy and also recorded from Sardinia, the Yugoslavian coast, Bulgaria and the Ukraine.



Figs 115–120 Oscillograms at three different speeds of the calling songs of two males of *Platycleis montana*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 3).



Figs 121–125 Oscillograms at three different speeds of the male calling song of *Platycleis stricta*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 3).

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I am particularly grateful to my colleague Mr W. J. Reynolds, who made a number of the song recordings used in this study, helped me in reviewing the past literature on the songs, tested the identification key based on morphological characters and provided valuable comments at various stages in the preparation of the paper.

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